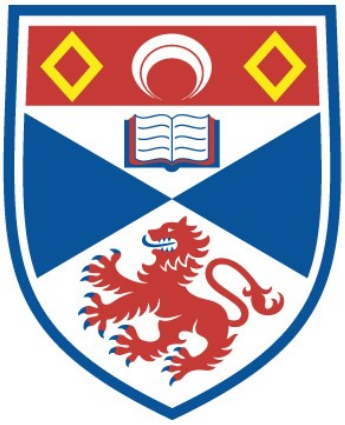
THE COMPARITIVE ANATOMY OF THE TECTUM OF THE MID-BRAIN

Probodh Ranjan Roy

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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THE COMPARATIVE ANATOMY OF THE TECTUM OF THE MID-BRAIN

BEING

A THESIS PRESENTED

BY

PROBODH RANJAN ROY

(B.Sc., M.B.,B.S.)

TO

THE UNIVERSITY OF ST.ANDREWS

IN

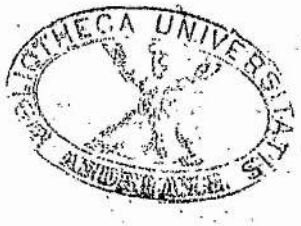
APPLICATION

FOR THE DEGREE

OF

DOCTOR OF PHILOSOPHY

October 1957



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DECLARATION

I hereby declare that the following Thesis is based on the results of experiments carried out by me, that the Thesis is my own composition, and that it is now re-submitted for a Higher Degree in accordance with the sanction granted by the Senatus Academicus in June 1957.

The research was carried out in the Department of Anatomy, Bute Medical Buildings, St. Salvator's College, St. Andrews.

(Probodh Ranjan Roy)

October 1957

CAREER

I matriculated in the University of Calcutta in 1933 and followed a course leading to graduation in Science (B.Sc.) in 1937 and in Medicine and Surgery (M.B., B.S.) in May 1944. After graduation I worked as a House Surgeon in the Maternity and Surgical wards of R.G. Kar Medical College and Hospitals for one and a half years and as Emergency Officer in the same Institution for about three years. Since 1949 I have been working as a Demonstrator of Anatomy in the Medical College, Calcutta.

On 1st September 1954 I commenced the research which forms the basis of this Thesis, under the supervision of Dr. J. Mulligan. The revised version of the Thesis has been completed by me on my return to Calcutta and is here submitted as a Ph.D. Thesis.

I was granted study leave by the Government of West Bengal from 1st August 1954 until March 1957.

(Probodh Ranjan Roy)

October 1957

CERTIFICATE

I certify that Probodh Ranjan Roy has spent nine terms at Research work in the Department of Anatomy, Bute Medical Buildings, St. Salvator's College, St.Andrews, under my supervision, that he has fulfilled the conditions of Ordinance No.16 (St.Andrews) and that he is qualified to submit the accompanying Thesis in application for the Degree of Doctor of Philosophy.

(John H. Mulligan)
M.B., Ch.B.

Lecturer in Neurology and Histology,
Department of Anatomy,
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St.Andrews.

October 1957

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The author also wishes to thank Professor Robert Walmsley, M.D., F.R.S.E., and the authorities of the University of St. Andrews for the provision of facilities extended to him to carry out this research in the Department of Anatomy, Bute Medical Buildings, St. Salvator's College.

(Probodh Ranjan Roy)

October, 1957.

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INTRODUCTION.

INTRODUCTION

Security is one of the cardinal requirements of living organisms, and the special senses of the body play a very important role in its maintenance. Of these special senses vision and hearing are the most important. This may have attracted the attention of many previous workers who have been led to carry out extensive researches on the part of the brain concerned with these two primary senses. In the vertebrate kingdom the midbrain is associated with these senses, and acts as an important centre for nervous correlation and co-ordination.

During the last 75 years researches have been carried out on the tectum of the midbrain in different vertebrates. These researches have been made from various aspects /

aspects - morphological, embryological, histological, physiological and histochemical. The author, however, has restricted his attention entirely to the gross anatomy and histology of the region. The gross anatomy of the part has previously been studied by R. Owen ('66, '68), G. Mivart ('81), A. Kappers ('06, '29), de Lange ('10), C.J. Herrick ('17), O. Larsell ('26, '29), A. Frederikse ('31), Huber and Crosby ('33), H.H. Charlton ('33), R.G. Meader ('34), Kappers, Huber, and Crosby ('36), E. Sutler ('43), A.S. Romer ('50), and J.Z. Young ('50). Most of the previous workers, however, have confined their researches mainly to the histology of the region, sometimes supplementing their observations by experiments. Amongst the pioneers in this work may be mentioned P. Ramón ('90, and '98), Ramón y Cajal ('91, '99, '09-'11), Ariëns Kappers ('06, '29), and Huber and Crosby ('33, '33a, '34). P. Ramón and Ramón y Cajal made their valuable observations almost entirely on material prepared by the Golgi method.

Most of the previous researches have been restricted to one or more specimens of a single species except for a few works relating to phylogeny by Huber and Crosby ('33, (33a,/

(33a, and '34).

In this thesis an attempt will be made to elucidate the comparative anatomy of the tectum of the midbrain as revealed by an examination of its gross anatomy and histology. Thus the external form of the tectum and the shape of the related part of the ventricular cavity will be studied. Special attention, however, will be given to the differences in the laminated arrangement of its nerve cells and fibres established by reference to Huber and Crosby's ('33) classification of the layers of the reptilian tectum.

In order to throw light on the significance of these differences they will be considered as evidence of the nature of the evolutionary changes which have given rise to the mammalian tectum. These changes will be compared with those taking place in the developing tectum of the chick with special reference to myelination. They will also be examined from a functional standpoint as suggested by Huber and Crosby's functional analysis (1933) of the reptilian tectum.

The author desires to make it clear that each of the /

the statements made under the heading of "observations" is based on his personal studies of the serial sections prepared, except where it has been specifically stated otherwise.

MATERIALS AND METHODS.

The materials consisted of 20 Salmo salar (salmon parr), 12 Rana temporaria temporaria (frog), 12 Lacerta viridis (common green lizard), 45 Gallus domesticus (domestic fowl), and 20 Mus norvegicus albinus (common white rat). These animals were selected for the work because they were easily available. The animals were all of adult ages except the birds whose ages varied from 1 day after hatching to 2 years or more.

The animals were killed with illuminating gas in a closed chamber, weighed, measured, and injected through the heart with 10% neutral formalin, and sodium chloride - 0.65% for the fish, frog, and lizard, 0.75% for the bird, and 0.85% for the white rat. The animals were then skinned and kept in the same fluid for preliminary fixation. After 48 hours each brain was removed from its cranial cavity, weighed, and several measurements were made as detailed later. The brains were then preserved in the same fixative for at least three weeks.

Photographs of the lateral surface of the adult brains of a fish, a frog, a lizard, and a bird were taken, together with that of a one day old chick, to show the different parts and their relative proportions. The/

The brain of an adult white rat was similarly photographed to show its dorsal surface. The tectum, being then exposed by the removal of the cerebrum and the cerebellum, was also photographed to show its lateral surface.

The brains were then embedded in paraffin by the following methods, which were found to be the most satisfactory:

Reagents/

Reagents	Fish (whole brain) - Adult.	Frog (whole brain) - Adult.	Lizard (whole brain) - Adult.	Bird (mid brain and parts of fore brain & hind brain)		White rat (mid brain and parts of fore brain & hind brain) Adult
				1 day old	Adult(2yrs.+)	
50% alcohol	2 hours	5 hours		5 hours	5 hours	
75% "	2 hours	15 "		15 "	15 "	
96% "	½ hour	1 hour (1 change)		3½ " (2 changes)	3½ " (2 changes)	
Absolute alcohol	½ hour	½ hour		1 hour	2 " (1 change)	
Chloroform	5 minutes	5 minutes		10 minutes	15 minutes	
Chloroform & paraffin	½ hour	½ hour		40 minutes	45 "	
Soft paraffin(49°C)	1 hour	1 hour		1 hour	1 hour	
Hard paraffin(54°C)	1 hour	1 "		2 hours	2 hours	
Embedding	Done →	→ 'Do' →		→ 'Do' →	→ 'Do'	

Remarks:

1. After a series of experiments the above time table was found suitable for embedding the respective brains in paraffin.

It was also noticed in the process of dehydration during embedding that the time in ascending grades of alcohol, /

Transverse sections were cut serially with a rotary microtome set for a thickness of 15 u. Every 5th section, having been mounted on a slide in the usual way, was stained to show the myelinated fibres by Goldman's method for protozoa (M. Goldman, '49). A similar series was stained with an acidified aqueous solution of a basic dye, carbol fuchsin, to show the Nissl granules contained in the cell bodies. A third series was stained by Bodian's silver technique (D. Bodian, '36, '37) to show the nerve cells and the neurofibrillae. These techniques were adopted since they could be standardised and applied to the same series of sections, as the research was meant to be a general survey of the comparative anatomy of the tectum. In particular, it may be noted that, although iron-haematoxylin techniques stain for the most part only the neurokeratin residue of the myelin sheaths, they provide an indication of the comparative degree of development of these sheaths. It was originally proposed to supplement the iron-haematoxylin with Pal-Weigert preparations, but the shortness of the time available made this impracticable. About 102 series of sections of the brains of different animals were thus stained by these different methods. Microphotographs of these sections were taken at three different levels viz. posterior commissure, oculomotor nucleus, and trochlear nucleus, to illustrate the observations as far as practicable.

alcohol, particularly 96% and absolute, should be cut down to the minimum by trial and error in order to prevent friability of the embedded tissue. Lower grades of alcohol, 50% and 75%, however, do not harm the tissues.

Furthermore, the clearing agent, Cedar-wood oil, was dispensed with, for it was found that the histogical pictures were not definitely improved by its use. Besides, it also helped in the economy of time.

2. In spite of all the above precautions, while cutting the sections with the rotary microtome, it was occasionally found necessary to apply Baker's fluid to the cut surface of the paraffin block to produce even and uniform sections without cracks or fissures.
3. The sections, mounted on albuminised slides and dried in the usual way, tended to come off the slides in aqueous solutions. Experiments were then carried out to overcome this difficulty:

Expt. I:

The sections were floated in a solution of 1% gelatin in water and mounted on clean dried slides. They were then exposed to formaldehyde vapour for

a/

a period of about 6 - 12 hours to coagulate the gelatin. This method, though quite efficient, had to be abandoned because the gelatin sticking on the slides took up the stains sufficiently to obscure the histological details.

Expt. II:

The sections were then mounted on albuminised slides by floating them on 75% alcohol and were kept on a hot plate so that the albumin was rapidly coagulated. This method, too, though otherwise satisfactory, was given up because of the violent movements of the sections while floating on alcohol. These movements were a hindrance to mounting the sections serially.

Expt. III:

The sections were once again floated on water, and dried in the usual way, being mounted on albuminised slides. The sections, after being deparaffinised with xylene and washed with absolute alcohol, were coated with 1.5% solution of celloidin in equal parts of absolute alcohol and ether and kept in 75% aqueous solution of alcohol for a few minutes/

minutes to help the formation of a gel. The subsequent steps were as usual. This method was found to be very satisfactory and was followed throughout the work.

4. Different basic dyes viz., Thionin, Methylene blue, Cresyl violet and Gallocyanin, were tried to show the Nissl granules; but the Carbol fuchsin method was found to be the best.

Similarly Goldmann's method for protozoa was adopted for this work to demonstrate the myelinated fibres because of the simplicity of the process. Many other methods were also tried but were given up because of their complexity or the difficulty of controlling the differentiation which made it difficult to standardise the process for the staining of the different series.

5. Experiments were also carried out with different methods of silver for staining in bulk and for paraffin sections; but the best results were obtained by Bodian's silver technique, particularly for the paraffin sections, which was of advantage for serial studies. Most of the other methods were unsuitable/

suitable for the purpose, either because of the patchy staining or undue precipitation of silver on the sections during reduction.

OBSERVATIONS
ON THE REPRESENTATIVE BRAINS
OF THE VERTEBRATE SERIES
AND
REVIEWS OF THESE OBSERVATIONS.

Class	-	Pisces.
Sub-class	-	Actinopterygii.
Order	-	Teleostei.
Sub-order	-	Salmonidae.
Species	-	Salmo salar. (salmon parr). (Age-3 yrs. +).

MEASUREMENTS.

I. (a) Length of the fish - 14.4 cm.

(b) " " " brain - 1.4 cm.

II. (a) Weight of the fish - 27.0 gms.

(b) " " " brain - 0.19 gms.

III. Optic lobe:

(a) Antero-posterior - 5.5 mm.

(b) Transverse - 3.5 mm.

(c) Supero-inferior - 4.0 mm.

IV. Cerebrum:

(a) Antero-posterior - 4.0 mm.

(b) Transverse - 1.5 mm.

V. Cerebellum:

(a) Antero-posterior - 5.0 mm.

(b) Transverse - 3.0 mm.

MACROSCOPIC OBSERVATIONS.

The **optic lobe** is very well developed in this form and is the most prominent feature of the brain. It is ovoid in shape being longest in its antero-posterior axis./

axis. The lobes are placed one on each side of the median plane, a longitudinal sulcus intervening between them dorsally. The large size of the lobes is well shown in the photograph (Fig. 1).

Each lobe measures 5.5 mm. antero-posteriorly, 3.5 mm. transversely, and 4.0 mm. supero-inferiorly. Each has got six surfaces - anterior, posterior, superior, inferior, medial, and lateral. The anterior surface is small and vertical, and lies in contact with the posterior surface of the corresponding cerebral hemisphere, a deep fissure intervening between them. The posterior surface is flat and vertical and is in contact with the cerebellum, which extends a little on to the superior surface of the optic lobe. The superior and the lateral surfaces are convex in all directions and are free. The inferior surface is also convex in all directions and is limited medially by a groove, called the sulcus limitans optici, which also encircles the lobe and demarcates it from the surrounding parts. The medial surface is fused with its fellow of the opposite side superiorly; inferiorly, however, it is fused with the diencephalon rostrally and the rhombencephalon caudally.

Each/

Each lobe contains a cavity, called the optic ventricle (Fig. 2). The optic ventricle is very wide and communicates supero-medially with its fellow of the opposite side and also with the aqueduct of the midbrain. It divides the optic lobe into a thin roof, called the optic tectum, since its function is primarily visual in the fish, and a relatively thicker floor, the torus semicircularis, which is continuous with the tegmentum of the mesencephalon. The optic ventricle extends posteriorly up to the caudal limit of the optic lobe with the torus semicircularis lying in its floor and not reaching the median plane, as in the frog and the lizard.

Superomedially the optic tectum protrudes into the optic ventricle in the form of a process which fuses rostrally with its fellow of the opposite side in the median plane forming an elevation into the ventricle, called the torus longitudinalis. Caudally, however, the two parts of the torus longitudinalis remain separate. This is a structure conspicuous in the fish. The valvula of the cerebellum is a median and rostral projection of its basi-auricular part (Kappers, '29) into the cavity of the optic ventricle where it lies ventral to the torus longitudinalis. It fuses with the eminentia media/

media of the torus semicircularis on each side and separates the aqueduct from the optic ventricle. Its median position and fusion with the torus semicircularis have probably prevented the latter approaching the median plane to undergo fusion with its fellow of the opposite side as in the frog and the lizard. Its size is in inverse proportion to that of the torus semicircularis (Kappers, Huber, and Crosby, '36).

MICROSCOPIC OBSERVATIONS.

A. OPTIC TECTUM.

The investigators of the teleost optic tectum have not agreed as to the number of its layers as may be seen from the following list:

1. Steida (1875) - 5 layers.
2. Fritsch (1878) - 8 layers.
3. Fusari (1887) - 7 layers.
4. P. Ramón (1890 & 1899) - 10 layers.
5. van Gehuchten (1894) - 6 layers.
6. Neumayer (1895) - 7 layers.
7. Ramón y Cajal (1911) - 10 layers.
8. Silvano Leghissa (1955) - 7 layers.

Fusari,/

Fusari, Ramón, van Gehuchten, and Neumayer made their studies on Golgi preparations.

The author's histological studies, based especially on the carbol-fuchsin and silver preparations, have shown the presence of 10 layers in salmo salar (salmon parr). The layers have been named from without inward as follows (Fig. 3):

(i) Layer 1 - stratum zonale.
(ii) Layer 2 - stratum opticum.
(iii) Layer 3 - Cell layer
(iv) Layer 4 - Fibre layer
(v) Layer 5 - Cell layer
(vi) Layer 6 - Fibre layer
= stratum fibrosum et griseum superficiale.
(vii) Layer 7 - Stratum griseum centrale.
(viii) Layer 8 - Stratum album centrale.
(ix) Layer 9 - Stratum griseum periventriculare.
(x) Layer10 - Stratum ependymale.

In making the above classification of the layers of the optic tectum the author has been influenced by the functional classification of Huber and Crosby ('33, '33a, and '34) on the reptilian and other submammalian optic tecta as may be seen from table 1 in which some of the other classifications, too, have been compared.

Table 1./

Table 1. Comparison of the author's classification of the layers of the optic tectum with that of other workers.

Number of layers	Author's Observations	Huber & Crosby ('33, '33a, '34)	P. Ramón & Ramón y Cajal ('90 & '11)	Silvano Leghissa ('55)
1	Stratum zonale	-	-	(7) Stratum fibrosum marginale.
2	Stratum opticum	→ (1) 'Do'	Layer (10)	Stratum plexiformum et fibrosum externum. (6)
3	Cell layer		Layer (9)	
4	Fibre layer	→ (2) 'Do'	Layer (8)	
5	Cell layer (Stratum fibrosum et griseum superficiale)		Layer (7)	(5) Stratum griseum externum.
6	Fibre layer		Layer (6)	(4) Stratum plexiforme internum.
7	Stratum griseum centrale	→ (3) 'Do'	Layers (4 & 5)	(3) Stratum griseum internum.
8	Stratum album centrale	→ (4) 'Do'	Layer (3)	(2) Stratum fibrosum profundum.
9	Stratum griseum periventriculare	(5) Stratum griseum periventriculare (6) Stratum fibrosum periventriculare	Layer (2)	(1) Stratum griseum periventriculare.

10/

Table 1. (Cont'd.)

Number of layers	Author's Observations	Huber & Crosby ('33, '33a, '34)	P. Ramón & Ramón y Cajal ('90 & '11)	Silvano Leghissa ('55)
10	Stratum ependymale	-	Layer (1)	(1) Stratum griseum periventriculare

Carbol-fuchsin preparations (Fig.4)

Layers 1 to 8:

All these layers have been considered together as the cells are so scattered and isolated that description of the individual layers is not possible. The cells consist of the following types, in order of their frequency:

(i) pyramidal,

(ii) fusiform, and

(iii) stellate.

The pyramidal cells predominate and form by far the largest group. Their long axes are directed mostly at right angles to the surface. The other types are distributed very irregularly.

Besides the cells, a few small round and oval nuclei without any stained or apparent cytoplasm and containing single or multiple particles are scattered throughout the layers. These nuclei, many of which probably belong to neuroglial cells, will hereafter be referred to as "nuclei without apparent cytoplasm".

Dorsally the layers are represented in the middle line by the relatively clear dorsal zone of the torus longitudinalis and are in direct continuity with the latter caudally (Fig.5). Ventrally and rostrally they are separated from the dienoephalon by a narrow linear zone /

zone of small cells and nuclei which are continuous with the nucleus corticalis (Fig. 6) (Fritsch, '78; Ariëns Kappers, '06, and Holmgren, '20). Further caudally they are limited ventrally by the sulcus limitans optici and by a few cells and nuclei of the stratum griseum periventriculare as well (Fig. 5). The layers become thinner dorsally and ventrally in the caudal region of the optic tectum.

Layer 9:

This is the broadest zone of nuclei and cells forming about half to one third the total width of the optic tectum. The nuclei and cells are very closely packed together, except ventrally where towards the ventricular side there are present irregular spaces between them. Cells with detectable cytoplasm are fewer in number and belong mostly to the small pyramidal type. The nuclei, like those of the previous layers, are small, round and oval in shape and form the chief constituents of the layer. They are more deeply stained than those of the superficial layers already described.

Dorsally the layer is represented by the richly nucleated ventral zone of the torus longitudinalis from which it is separated by a slit like diverticulum of the optic/

optic ventricle and its well marked ependymal layer. Caudally it is fused with the valvula of the cerebellum. Ventro-medially, however, it merges with the torus semicircularis (Fig. 5).

Layer 10:

Caudally this layer is very indefinite, but rostrally it consists of 2 to 4 rows of closely packed nuclei which are either round like those of layer 9, or oval in shape with their long axes at right angles to the ventricular surface. In some sections there are villous like projections of this layer into the cavity of the optic ventricle. The layer is separated from the previous layer (i.e. layer 9) by a narrow space, presumably the rudiment of the stratum fibrosum periventriculare of the still higher forms (Fig. 2).

There is a little thickening of the layer in the median plane of the roof of the ventricle at the level of the posterior commissure. This is the subcommissural organ of Dendy and Nicholls ('10) and is so called because it lies deep to the commissure (Fig. 6).

Iron-haematoxylin preparations.

The/

The iron-haematoxylin staining of the myelinated fibres of the fish optic tectum proved very difficult and the following observations should not be regarded as satisfactory.

Layer 1:

No fibres have been stained in this layer.

Layer 2:

This layer presents a few scattered bundles of very faintly stained myelinated fibres disposed mostly transversely. Dorso-medially and ventro-laterally the layer seems to merge with the tractus opticus marginalis pars medialis and tractus opticus marginalis pars lateralis respectively. The fibres are more evident ventrally than dorsally.

Layers 3 to 7:

No fibres can be seen in these layers.

Layer 8:

A few strands of ill defined fibres, cut into different lengths, are disposed in the layer mostly transversely. Rostrally at the level of the posterior commissure the fibres of the layer seem to pass dorsally through the torus longitudinalis to form the commissura tecti. Ventrally, however, the fibres take a sudden inward turn in small isolated bundles. They are cut into short lengths, and /

and enter the next deeper layer (layer 9) on their way to the tegmentum. The direction of the fibres suggests that rostrally they pass to the opposite side through the posterior commissure; caudally, however, some of them come into relationship with the neurons of the torus semicircularis while others curve ventro-medially and enter the tegmentum forming the different tecto-bulbar and the tecto-tegmental tracts. The ventral tecto-bulbar tract appears as a large bundle of fibres, which, sweeping on to the lateral and the ventral aspect of the tegmentum crosses to the opposite side in the ventral tegmental decussation. Still further caudally a few fibres can be seen to enter the valvula of the cerebellum, and are thus tecto-cerebellar in character.

Layer 9:

There are no fibres in the dorsal part of this layer, but in the ventral part there are a few small bundles, cut into very short lengths. These bundles, in fact, enter this layer from layer 8 on their way to the tegmentum.

Layer 10:

This layer does not contain any fibres.

Silver Preparations.

In/

In the silver preparations the fibres show very distinctly.

Layer 1:

This layer presents ventro-laterally a few bundles of transverse fibres which merge with the tractus opticus marginalis pars lateralis (Fig.6). Occasional radial fibres from the deeper zone can also be seen to enter this layer.

Layer 2:

It contains chiefly a few bundles of transverse fibres, cut into different lengths and present mostly in the ventral half of the layer; dorsally, however, the fibres are distributed obliquely. Dorso-medially and ventro-laterally the layer merges with the tractus opticus marginalis pars medialis and tractus opticus marginalis pars lateralis respectively. The radial fibres from the deeper zones enter this layer freely.

Layers 3 to 6:

Layer 3 contains scattered radial and transverse fibres. /

fibres. Some of the radial fibres from the deeper zones enter this layer and some again pass through it into the next superficial layer, as described already. The trans: :verse fibres, from their arrangement and distribution, seem to belong to the marginal optic tract. The layer contains also a few scattered round and oval nuclei without apparent cytoplasm.

Layer 4 resembles layer 2 in all respects - in width and in arrangement and distribution of its fibres.

Layer 5 is very similar to layer 3 in all its characteristics except that the scattered cells and nuclei are more numerous.

Layer 6 resembles layers 2 and 4 in the arrangement and distribution of the fibres; but it is a little broader than the other layers and its fibres, particularly the transverse ones, are more scattered.

Layer 7:

This layer resembles layers 3 and 5; but it is about twice as broad as either.

All the layers from 1 to 7 converge dorso-medially and are continuous with the superficial dorsal zone of the torus longitudinalis (Fig.5).

Layer 8:

This /

This layer is conspicuous being the broadest of all the fibre layers of the optic tectum. The layer is narrower dorso-medially but broader ventro-laterally. It consists of both transverse and radial fibres, the former predominating and forming the most characteristic feature of the layer. The ventral zone of the layer presents in addition, however, a plexiform network (Fig. 6).

Rostrally at the level of the posterior commissure the general drift of the transverse fibres indicate that dorso-medially they cross to the opposite side through the torus longitudinalis forming the commissura tecti. Ventrally midway between the dorsal and the ventral borders of the optic tectum they bend inwards in isolated short bundles to reach the tegmentum passing through layer 9. Some fibres appear to cross to the opposite side in the posterior commissure (Fig. 6). Some, on the other hand, bend ventro-medially and decussate in the dorsal supra-optic decussation, while others come into relationship with some of the neurons of the diencephalon (e.g. of the pretectal and of the dorsal thalamic nuclei).

Caudal to the posterior commissure the fibres still seem to cross to the opposite side in the commissura tecti/

tecti in the roof of the optic ventricle through the torus longitudinalis; but further caudally where the two halves of the torus longitudinalis remain separated this dorsal crossing of fibres stops short. Ventrally, on the other hand, as already described, small bundles of fibres run medially emerging from this layer approximately midway between its dorsal and ventral borders. They enter the tegmentum passing through layer 9 in isolated short bundles (Fig.3). These fibre bundles increase in number in the rostro-caudal direction and form the dorsal and the ventral tecto-bulbar tracts. The ventral tecto-bulbar tract is larger and more conspicuous than the dorsal and at the level of the oculomotor nerve and its nucleus forms a well marked bundle which runs close to the lateral and ventral surfaces of the tegmentum (Fig.7). Both these tracts decussate in the middle line in the dorsal and the ventral tegmental decussations respectively as tractus tecto-bulbaris dorsalis cruciatus and tractus tecto-bulbaris ventralis cruciatus. Besides, the fibres of the dorsal tecto-bulbar tract further come into intimate relationship with the neurons of the torus semicircularis (nucleus lateralis mesencephali) of the same side. They are also connected with the fibres /

fibres of the fasciculus longitudinalis medialis (medial longitudinal bundle), which, on the other hand, are very closely related to both the oculomotor and the trochlear nuclei. It is perhaps through the fasciculus longitudinalis medialis that the optic tectum establishes its connections indirectly with the oculomotor and the trochlear nuclei. A few fibres, however, enter the ventral aspect of the valvula of the cerebellum. These fibres are in line with the others which emerge from the optic tectum of the same side between the dorsal and the ventral tecto-bulbar tracts and are to be regarded as tecto-cerebellar pathways.

The radial fibres enter the superficial as well as the deeper layer.

Layer 9:

Dorsally /

Dorsally the layer does not show any fibres, but ventrally there are some small bundles, cut into short lengths. These bundles, in fact, as stated already, are derived from the previous layer (i.e. layer 8) and are on their way to the tegmentum. Ventrally there are a few radial fibres which are continuous with similar fibres of the superficial layers and have already been described.

Layer 10:

No fibres are present in this layer.

B. TORUS SEMICIRCULARIS.

It is formed by the grey matter in the floor of the optic ventricle (Fig. 2). The form and size of this grey matter depend upon the development of the vestibular and of the lateral line system, and vary greatly in different teleosts (Kappers, Huber, and Crosby, '36). It maintains this position in the floor of the optic ventricle throughout its rostro-caudal extent and lies hidden from the surface by the optic tectum. Its position is greatly influenced by the development of the valvula of the cerebellum (Kappers, Huber, and Crosby, '36). Rostrally it is very ill defined; a little caudally, however,/

however, just before its fusion with the valvula of the cerebellum its ventricular surface presents two eminences, the medial and the lateral, being separated from each other by a shallow ventricular groove (Fig.5). The medial eminence, or the eminentia media, fuses with the valvula of the cerebellum. The lateral eminence, however, is more developed. It contains the nucleus lateralis mesencephali and forms a marked projection into the optic ventricle. The fusion of the valvula of the cerebellum with the eminentia media of each side (Fig.7) has not only separated the aqueduct from the optic ventricle, but has also prevented the two tori semicirculares, unlike the condition in the frog and the lizard, approaching the median plane to undergo fusion with each other.

Carbol-fuchsin preparations

The cells and nuclei resemble those of the optic tectum. The cells are predominantly of the pyramidal type. Some fusiform and a few stellate cells are also present. The nuclei are without any apparent cytoplasm and are small round and oval in shape containing single or multiple particles.

Rostrally /

Rostrally at the level of the posterior commissure where it is ill defined, it consists of (i) a thin, dorso-lateral peripheral capsular zone consisting of closely packed cells and nuclei which lie just beneath the ependymal lining of the floor of the optic ventricle and merge ventro-laterally with the ventral part of the stratum griseum periventriculare (or layer 9) of the optic tectum, and (ii) a broad ventro-medial central zone where the cells and nuclei are either very loosely scattered or, are arranged into very small groups (Fig. 2).

Further caudally just before the fusion of its eminentia media with the valvula of the cerebellum (Fig. 4) the capsular part of the eminentia media forms a narrow dorsal zone consisting of 2 to 3 rows of cells and nuclei situated parallel to the ventricular surface from which it is separated by a well defined space; laterally it is continuous with a similar zone of the nucleus lateralis mesencephali; in the ventral zone, however, the cells and nuclei are loosely scattered. The lateral eminence, on the other hand, presents a well marked aggregation of neurons, called the nucleus lateralis mesencephali; the peripheral capsular part of the nucleus consists of closely/

closely packed cells and nuclei and limits the deeper ventral area not only dorsally and laterally, as already stated, but also dorso-medially to a certain extent; it is deficient, however, ventrally; laterally the capsular zone demarcates the nucleus from layer 9 of the optic tectum dorsally, but ventrally they are continuous; the deeper ventral zone consists of cells and nuclei which are scattered either very diffusely, or are arranged into very small groups and merges ventrally with the tegmentum and medially with a similar zone of the eminentia media.

Still further caudally where the eminentia media is fused with the valvula of the cerebellum and at the level of the oculomotor nucleus the nucleus lateralis mesencephali is very well defined; the peripheral capsular zone is very prominent but is deficient ventro-laterally; the deeper central (ventral) zone, consisting of cells and nuclei either scattered or arranged into groups, merges with the tegmentum ventro-laterally where the capsular zone is deficient; ventro-medial to this nucleus and lateral to the fasciculus longitudinalis lateralis (acoustico-lateral lemniscus) lie the scattered cells and nuclei of the nucleus profundus mesencephali; dorsal to the nucleus profundus mesencephali at the level of the oculomotor/

oculomotor nucleus is situated the nucleus isthmi consist: ;ing of a central semilunar and an incomplete peripheral zone of closely packed cells and nuclei, the cells being mostly of the pyramidal type, not being differentiated into the magnocellular and parvocellular parts. At the site of fusion of the valvula of the cerebellum with the eminentia media (of the torus semicircularis) there is a great aggregation of cells and rounded nuclei without any cytoplasm called the nucleus lateralis valvulae of Herrick ('05), which is continuous with the granular layer of the cerebellum. The cells of the eminentia media lie on the ventral aspect of the nucleus lateralis valvulae; medially these neurons form a continuous line with the oculomotor nucleus.

Iron-haematoxylin preparations

The staining of the myelinated fibres is so poor and indefinite that no effective study is possible in these preparations.

Silver preparations

Most rostrally where it is very ill defined i.e. prior to its differentiation into the medial and the lateral eminences the fibres of the plexiform network of the /

the torus semicircularis are in direct continuity with those of the dorsal tecto-bulbar tract. It is very probable that the network is also continuous with its fellow of the opposite side through the posterior commissure.

Further caudally where it is differentiated into its medial and lateral eminences (Fig.3) the plexiform network of fibres of the nucleus lateralis mesencephali is not only continuous with the fibres of the dorsal tecto-bulbar tract, as stated already, but also with the similar network of the medial eminence of the same side and probably is further connected with its fellow of the opposite side through the dorsal tegmental decussation bringing about thereby a bilateral correlation between the two tori semicirculares.

Still further caudally at a level where the eminentia media fuses with the valvula of the cerebellum the network of fibres in relation to the nucleus lateralis mesencephali is directly continuous with the fasciculus longitudinalis lateralis /

lateralis (acoustico-lateral lemniscus). Furthermore, the fibres of the tecto-bulbar tract, as already described, can still be found to enter it.

The nucleus lateralis valvulae, on the other hand, is traversed by the fibres of the tractus mesencephalo-cerebellaris posterior.

C. TORUS LONGITUDINALIS.

It is a median structure which projects into the optic ventricle from its roof and blends on each side with the optic tectum. Its shape in cross section varies at different levels. Rostrally it is triangular in shape with its apex directed upwards and base downwards (Fig. 6). The apex gradually flattens out in the rostro-caudal direction. The flat base, on the other hand, fuses rostrally with the dorsal surface of the posterior commissure but further caudally it protrudes into the optic ventricle at first as a free convex surface changing still further caudally into a conical projection (Fig. 2) which finally presents a notch (Fig. 5) in the median plane of its ventricular surface; the notch gradually extends upwards/

wards dividing ultimately the torus longitudinalis into two halves, each of which is attached to the respective optic tectum. It is, thus, probably very true that the torus longitudinalis arises by the fusion in the median plane of the overgrowing processes of the dorso-medial parts of the respective optic tectum projecting into the optic ventricle. Rostrally a fold of pia mater dips into it in the median plane dorsally. Caudally, however, no such septum is visible.

Carbol-fuchsin preparations

It can be easily DIVIDED into two zones: (i) a small relatively clearer dorsal zone, and (ii) a larger ventral zone consisting chiefly of closely packed and deeply stained nuclei without apparent cytoplasm and a few cells.

The smaller dorsal zone presents a few scattered large rounded cells containing distinct round or oval nuclei. These cells, however, are more aggregated at the junction between the dorsal and the ventral zones constituting a so-called junctional zone. Caudally the zone is continuous laterally with the more superficial layers of the optic tectum (i.e. layers 1 to 8).

The ventral zone is relatively larger than the dorsal one /

one consisting of closely packed and deeply stained nuclei and cells like those of layer 9 of the optic tectum. Laterally it is limited by a slit like dorsal extension of the optic ventricle having a thick and dense ependymal lining. Rostrally the zone is continuous with layer 9 of the optic tectum.

These preparations thus suggest that the torus longitudinalis is a projection into the optic ventricle of the superomedial part of the optic tectum which has fused in the median plane with its fellow of the opposite side. It has, further, been suggested that structurally it resembles the cerebellum in that it has also three layers like the cerebellar cortex (Kappers, Huber, and Crosby, '36).

Iron-haematoxylin preparations.

No distinct fibres are visible in these preparations except one or two, very faintly stained and disposed horizontally in the deeper part of the relatively clearer dorsal zone. These fibres probably belong to the commissura tecti and seem to be continuous on each side with those of layer 8 of the optic tectum.

Silver preparations./

Silver preparations.

A few fibres can be seen in the deeper part of the dorsal zone. The fibres are cut into different lengths and are distributed transversely across the torus longitudinalis. The fibres belong to the commissura tecti and are continuous on each side with those of layer 8 of the optic tectum.

REVIEW OF THE OBSERVATIONS.

1. The optic lobe is very well developed and is the largest part of the brain. Its size in relation to that of the cerebrum and the cerebellum is quite apparent in the photographs. It lies in contact with the cerebrum and the cerebellum, but is not overlapped by them. The cerebrum, is very poorly developed and presents a smooth surface. The cerebellum is well developed; its surface is smooth and its basi-auricular part projects rostrally into the optic ventricle forming the valvula of the cerebellum.
2. The two lobes are apposed to each other in the median plane, a median longitudinal sulcus intervening between them dorsally; below the sulcus the lobes are fused with/

with each other. Ventrally, however, they are fused with the diencephalon, the tegmentum of the mesencephalon and the rostral part of the rhombencephalon (from before backward).

3. Each lobe is encircled by a circular sulcus, the sulcus limitans optici, which demarcates the lobe from the surrounding parts.

4. Each lobe contains a cavity, the optic ventricle, which appears to be the lateral extension of the aqueduct. The optic ventricle thus communicates with the aqueduct and with its fellow of the opposite side as well. It divides the optic lobe into a thin walled roof, the optic tectum, and a floor, the torus semicircularis, which is continuous ventrally with the tegmentum of the mesencephalon. The lateral recess of the optic ventricle differentiates the roof from the floor laterally and does not represent the position of the sulcus limitans of the aqueduct, which, however, is very indefinite in this form.

The ventricle extends caudally up to the caudal limit of the optic lobe and is separated from the aqueduct caudally by the fusion of the valvula of the cerebellum with the eminentia media of the torus semicircularis./

circularis.

5. The supero-medial part of the optic tectum projects into the optic ventricle in the form of a distinct process, which, fusing with its fellow of the opposite side in the median plane forms the torus longitudinalis, a structure characteristic of the fish.

6. The torus semicircularis, throughout its rostro-caudal distribution, lies in the floor of the optic ventricle under cover of the optic tectum. It is differentiated into the eminentia media and the eminentia lateralis which are demarcated by a groove on its ventricular surface. It does not approach the median plane to undergo fusion with its fellow of the opposite side; its eminentia media, however, fuses with valvula of the cerebellum.

7. Optic tectum.

(A) Histological examinations have revealed 10 layers which have been named from without inward. The lamination of the more superficial layers (i.e. 1 to 8), though indefinite, is more pronounced in this form than in the frog. The stratum fibrosum et griseum superficiale consists of 4 alternate cell and fibre layers. The stratum griseum centrale/

centrale is very ill defined. The stratum griseum periventriculare forms a conspicuous broad zone consisting of closely packed and deeply stained cells and nuclei. The stratum fibrosum periventriculare, as an independent layer, is not visible. The stratum ependymale is very indefinite caudally.

(B) Cyto-architecture.

(a) The optic tectum can be divisible broadly into two zones: (i) a periventricular inner zone (layer 9) consisting of closely packed and more deeply stained nuclei and cells, and (ii) a relatively clearer outer zone (layers 1 to 8) containing scattered cells and nuclei, less deeply stained and arranged into indistinct layers.

(b) The cells are usually of three types - pyramidal, fusiform, and stellate in order of their frequency of occurrence.

(c) Dorsally layers 1 to 8 merge with the relatively clearer dorsal zone of the torus longitudinalis, while ventrally they are limited partly by the sulcus limitans optici and partly by the nuclei and/

and cells of layer 9.

(d) The nuclei and cells of layer 9, on the other hand, are represented and, in fact, are continuous dorsally with the similar richly nucleated and cellular ventral zone of the torus longitudinalis, while ventrally they merge with those of the torus semicircularis.

(e) The subcommissural organ appears at the level of the posterior commissure as a thickening of the ependymal layer by proliferation of its nuclei in the median plane of the roof of the ventricle.

(C) Fibro-architecture.

(a) The fibres of the optic tectum are for the most part non-myelinated. A few faintly stained myelinated fibres are present in layers 2 and 8.

(b) The transverse fibres of layers 2, 4, and 6, have the same arrangement and distribution and merge with the tractus opticus marginalis pars medialis et lateralis.

(c) The transverse fibres of layer 8. Dorsally they decussate to the opposite side in the roof of the ventricle forming the commissura tecti. Ventrally some of these fibres decussate in the posterior commissure; the rest enter the tegmentum forming the tecto-bulbar, tecto-

tegmental /

tegmental, tecto-toral, and tecto-isthmal tracts. The tecto-bulbar and the tecto-tegmental tracts further decussate in the median plane in the supra optic and the dorsal and the ventral tegmental decussations. Through these fibres the optic tectum comes into relationship with the different diencephalic and tegmental neurons of the same as well as of the opposite side bringing thereby a widespread bilateral correlation. Further the dorsal tecto-bulbar tract connects the optic tectum with the oculomotor and the trochlear nuclei of the same side either directly, or indirectly through the fasciculus longitudinalis medialis with which it is very intimately connected. The tecto-toral and tecto-isthmal tracts, on the other hand, connect the optic tectum with the torus semicircularis and the nucleus isthmi of the same side. The optic tectum is also connected with the valvula of the cerebellum by the tecto-cerebellar tract.

(d) The radial fibres are distributed throughout the different layers of the optic tectum.

8. /

8. Torus longitudinalis

(A) As stated already it is a median structure which projects into the optic ventricle from its roof and is formed by the fusion of two separate processes from the dorso-medial part of the optic tectum. Rostrally it is fused by its base with the dorsal surface of the posterior commissure.

(B) Cyto-architecture.

(a) It has two distinct zones:

(i) a smaller relatively clearer dorsal zone consisting of very few cells and nuclei which resemble and merge with the more superficial layers of the optic tectum (i.e. layers 1 to 8); there are present also a few large round cells which are more aggregated between the dorsal and the ventral zones forming a so-called junctional, or /

or intermediate zone, and

(ii) a larger ventral zone consisting of closely packed and more deeply stained cells and nuclei which resemble those of layer 9 of the optic tectum being, in fact, continuous with the latter.

(C) Fibro-architecture.

(a) A few transverse fibres, mostly non-myelinated, are present between the dorsal and the ventral zones and are continuous laterally with similarly disposed fibres of layer 8 of the optic tectum.

9. Torus semicircularis.

(A) Cyto-architecture.

(a) The lateral eminence contains the nucleus lateralis mesencephali which consists of:

(i) a peripheral capsular zone of closely packed cells and nuclei, deficient ventrally and continuous laterally with the similar cells and nuclei of the periventricular layer (layer 9) of the optic tectum, and

(ii) a central area consisting of scattered cells and nuclei which merge ventrally with the tegmentum; the cells are mostly pyramidal in/

in character, some fusiform and occasional stellate cells are also present.

(b) The eminentia media also consists of a dorsal capsular zone and a ventral area. These resemble and merge respectively with the capsular and the central area of the nucleus lateralis mesencephali.

(c) At the site of fusion of the valvula of the cerebellum and the eminentia media of the torus semicircularis lies the nucleus lateralis valvulae which is represented by an elongated area of closely packed and more deeply stained nuclei and cells resembling those of the granular layer of the valvula of the cerebellum and layer 9 of the optic tectum.

(B) Fibro-architecture.

(a) The torus semicircularis consists of a dense plexiform network of fibres, which are mostly non-myelinated in character.

(b) The network is connected with the fasciculus lateralis longitudinalis (acoustico-lateral lemniscus). /

(c) The network is further connected with the tecto-bulbar tract of the same side.

(d) Furthermore, the network is continuous with its fellow of the opposite side through the dorsal tegmental decussations.

Class - Amphibia.

Sub-class - Euamphibia.

Order - Anura.

Sub-order - Phaneroglossa.

Species - Rana temporaria temporaria.
Age - 3 yrs.(+)

MEASUREMENTS.

I. (a) Length of frog (female) - 6.3 cm.

(b) " " brain - 1.0 cm.

II. (a) Weight of frog - 17.5 gm.

(b) " " brain - 0.06 gm.

III. Optic lobe.

(a) Antero-posterior - 2.0 mm.

(b) Transverse - 3.0 mm.

IV. Cerebrum.

(a) Antero-posterior - 5.0 mm.

V. Cerebellum.

(a) Antero-posterior - 0.5 mm.

(b) Transverse - 3.0 mm.

MACROSCOPIC OBSERVATIONS.

Each optic lobe is ovoid in shape. Each measures about 2 mm. antero-posteriorly and 3 mm. transversely. The lobes are placed obliquely, their longitudinal axes being directed, from above, downward, forward and outward. Dorsally they are apposed with each other, a medial sulcus intervening between them. Medially they are fused with each/

each other dorsally, but ventrally they remain separated from before backward by caudal part of diencephalon, tegmentum of mesencephalon and rostral part of rhombencephalon.

The exposed superficial surface of each lobe is smooth and convex in all directions and is covered by a very thin black and pigmented membrane, the pia mater. The lobes are not overlapped by the cerebrum or the cerebellum. They are separated from the cerebral hemispheres by the diencephalon which is distinctly evident both dorsally and ventrally. Posterior to them lies the cerebellum as a thin flattened structure being separated from them by a deep transverse cleft. The size of each lobe, as is evidenced from the photographs, is smaller than the cerebrum, but bigger than the cerebellum (Fig. 8).

Each lobe contains a cavity, called the optic ventricle, which is, in fact, the lateral extension of the aqueduct. The optic ventricle divides the optic lobe into a thin roof, the optic tectum, and a relatively thicker floor, the torus semicircularis, which is fused with the tegmentum of the midbrain (Fig. 9). The lateral recess of the optic ventricle does not represent the position of the sulcus limitans, which lies in the lateral wall of the aqueduct ventral to the torus semicircularis. The optic ventricle communicates/

communicates medially with its fellow of the opposite side and the aqueduct of the midbrain. Caudally, however, the aqueduct is completely separated from the optic ventricle by the fusion of the two tori semicirculares in the median plane. The optic ventricle does not extend caudally up to the caudal limit of the optic tectum, which extends from the level of the posterior commissure rostrally to the point of emergence of the trochlear nerve through the medullary velum caudally.

MICROSCOPIC OBSERVATIONS.

A. OPTIC TECTUM.

The internal structure of the midbrain of the tailless amphibia have been studied by many workers (Bellonci, '88; Gaupp, '89; P. Ramón, '96; Ariëns Kappers and Hammer, '18; Ariëns Kappers, '21; Larsell, '23, '31; Röthing, '23, '26, '27; Huber and Crosby, '33, '33a, and '34).

The author has observed 15 different layers in the optic tectum in frog. In naming and classifying these layers he is in complete agreement with Huber and Crosby ('33, '33a, and '34) who named the layers from without inwards/

inwards entirely free from a functional standpoint (Fig.10). In table 2 the author's observations have been correlated with those of Huber and Crosby ('33, '33a, and '34) and P. Ramon ('96).

Carbol-fuchsin preparations (Figs.9,11,12)

Layer 1 (stratum zonale):

A very few round and oval nuclei without any apparent cytoplasm and containing single or multiple particles are scattered here and there. Some of these nuclei are a little larger than the others.

Layer 2 (stratum opticum):

The layer resembles layer 1.

Layers 3 to 6 (stratum fibrosum et griseum superficiale):

Round and oval nuclei, described already, are scattered through all the layers of the stratum fibrosum et griseum superficiale. They are very scanty in layers 4 and 6, but they are more numerous in layers 3 and 5. The appearance of the somewhat indefinitely differentiated cytoplasm around these nuclei suggests that probably most of them belong to pyramidal cells.

Dorsally the layers are continuous with those of the opposite side along the roof of the ventricle, ventrally the cells lie scattered.

A few spindle shaped nuclei are also present here and there. These probably belong to the endothelial cells of /

Table 2. Comparison of the author's classification of the layers of the optic tectum with that of other workers.

Number of layers	Author's Observations	Huber and Crosby ('33, '33a, & '34)	P. Ramón ('96)
1	Stratum zonale (St.z.)	(1) 'Do' (Primordial)	Layers 13, 14, & 15.
2	Stratum opticum (St.o.)	(2) 'Do'	
3	Cell layer		Layer 12
4	Fibre layer (Stratum fibrosum et griseum superficiale (St.f.g.s.))	(3) 'Do'	Layer 11
5	Cell layer		Layer 10
6	Fibre layer		Layer 9
7	Stratum griseum centrale (St.g.c.)	(4) 'Do'	Layer 8
8	Stratum album centrale (St.a.c.)	(5) 'Do'	Layer 7
9	Outer granular layer	(6 & 7) Stratum griseum et fibrosum periventriculare	Layer 6
10	Outer plexiform layer		
11	Middle granular layer		
12	Inner plexiform layer		Layer 5
13	Inner granular layer		Layer 4
14	Stratum fibrosum periventriculare (St.f.p.)		Layer 3
15	Stratum ependymale (St.e.)	-	Layers 1 & 2

(Stratum griseum periventriculare (St.g.p.))

of the blood vessels.

Layer 7 (stratum griseum centrale):

This layer, too, presents many scattered nuclei as in the previous layer. Some of the nuclei as before are a little bigger than the rest; there is again only indefinite cytoplasmic differentiation. Most of these cells seem to be of the pyramidal type, but a few stellate cells are also present. The cells and nuclei are scattered diffusely in 6 to 7 rows and are separated by well spaced intervals.

Dorsally they are continuous with those of the opposite side along the roof of the ventricle, while ventrally they lie isolated and scattered.

A few fusiform nuclei, belonging probably to the endothelial cells of the blood capillaries, can also be seen here and there.

Layer 8 (stratum album centrale)

This is a relatively clear zone which contains only few scattered cells and nuclei as in the previous layers. Few large stellate cells are also present here /

here and there.

Layers 9 to 13 (stratum griseum periventriculare):

The stratum griseum periventriculare is the broadest zone of the optic tectum and presents the GREATEST cellular and nuclear density. The cells and nuclei are like those of the stratum griseum centrale and the other layers of the tectum, already described. Depending on their mode of distribution they are further differentiated into three indefinite zones- the outer granular layer or layer 9, the middle granular layer or layer 11, and the inner granular layer or layer 13, by two narrow plexiform layers of fine fibres or layers 10 and 12 as maybe seen from the silver preparations (Fig. 10).

Layer 9 consists of 4 to 5 rows of cells and nuclei, closely packed and more or less evenly distributed throughout the layer. Layer 11, on the other hand, is not uniformly thick - dorsally it is narrower consisting of 2 to 3 rows of closely packed cells and nuclei, while laterally and ventrally it is broader and resembles layer 9. In some of the sections layers 9 and 11 merge with each other laterally and ventrally. Layer 13, however, is the narrowest of all the layers and/

and consists of only 1 to 2 rows of closely packed cells and nuclei becoming even 3 to 4 rows deep ventrally. Dorsally all these layers converge at the roof of the ventricle and are continuous with those of the opposite side; ventrally they do so with those of the tegmentum and the torus semicircularis.

Layers 10 and 12 are relatively clear zones and contain scattered cells and nuclei. In iron-haematoxylin and silver preparations they present a plexiform network of fibres which will be described later in detail.

Layer 14 (stratum fibrosum periventriculare):

It is a narrow clear zone and contains a few scattered nuclei like those of the previous layers.

Layer 15 (stratum ependymale):

This layer consists chiefly of 1 to 3 rows of elongated nuclei containing many distinct particles, set at right angles to the ventricular surface. Some thread-like processes extend outward towards the surface in a radial manner from the peripheral aspect of these nuclei. These form the supporting tissue framework of the optic tectum. The sub-

commissural organ appears as proliferation of these nuclei at the level of the posterior commissure in the roof of the ventricle in the median plane.

Superficial to the ependymal nuclei there are one or two rows of nuclei like those of the granular layers, already described. Like the previous layers these probably also belong to the pyramidal cells. Dorsally they are continuous with those of the opposite side along the roof of the ventricle, while ventrally they do so with those of the torus semicircularis.

Mesencephalic nucleus of the trigeminal nerve:

The mesencephalic neurons of the fifth cranial nerve appear as large isolated cells, round or piriform in shape, chiefly amongst the cells and nuclei of layers 13 and 15. One or two cells can also be found in the deeper zone of layer 11. The cells are situated only in the region of the posterior commissure.

Iron-haematoxylin preparations.

Layer 1:

Small segments of few faintly stained fibres, disposed mostly transversely or obliquely, are scattered here and there. The fibres seem to be in a line with those/

those of layer 2 and are also probably optic in nature.

Layer 2:

This is a very narrow zone consisting of a network of fibres. The network is more evident in the ventral half of the layer, less so dorso-medially and very indistinct in the other parts. Dorsally and ventrally the layer merges with tractus opticus marginalis pars medialis and tractus opticus marginalis pars lateralis respectively. Occasional radial and oblique fibres from the deeper layers are seen to enter this layer.

Layers 3 to 6:

Layer 3 is much broader than layer 2 and consists of few scattered fibres, faintly stained and cut into short lengths. Nothing definite can, however, be made out regarding their distribution.

Layer 4 resembles layer 2.

Layer 5 corresponds with layer 3.

Layer 6 resembles also layer 2 except that it is a little broader than the latter and its fibre bundles are more distinct. Ventrally, however, unlike layer 2, some of its transverse fibres bend medially and enter the tegmentum.

Layer 7:

A/

A few transverse and radial fibres, cut into different lengths, are irregularly scattered throughout the layers, the former predominating particularly in its ventral half.

The transverse fibres are arranged into small bundles and are, in fact, in a line with those of layer 8; probably they belong to the latter, being also efferent in character. Ventrally they enter the tegmentum and are distributed along with the tectobulbar fibres.

The radial fibres, on the other hand, are very scanty and appear singly. They are continued into layer 6 superficially and layer 8 centrally.

Layer 8:

This layer, too, like the previous one, consists of transverse and radial fibres. The transverse fibres predominate markedly over the radial and constitute the most characteristic feature of the layer. Further they are conspicuous having the greatest density of staining and thickest myelin sheaths as compared with other layers of the optic tectum. The fibres are arranged /

arranged into small compact bundles. Dorsally and rostrally they decussate in the roof of the ventricle through the dorsal part of the posterior commissure. Further caudally they do so in the decussatio tecti mesencephali. Ventrally they enter the tegmentum and form the tecto-bulbar and tecto-tegmental tracts, which decussate ultimately in the median plane in the dorsal and the ventral tegmental decussations respectively. By the fibres of these tracts the optic tectum thus comes into relationship with the different tegmental neurons of the same side and probably also with the other. Besides, the fibres enter the homolateral torus semicircularis and nucleus isthmi. Moreover, they are connected with the oculomotor nucleus of the same side, but no such connection can be found with the trochlear nucleus. However, they are intimately connected with the fasciculus longitudinalis medialis which, perhaps, indirectly connects the optic tectum with the oculomotor and the trochlear nuclei.

The radial fibres, as usual, appear singly and enter the superficial as well as the deeper layers.

Layers 9 to 13:

These/

These layers consist of a plexiform network of fibres aggregated into two narrow zones i.e. layers 10 and 12, demarcating thereby the periventricular cells and nuclei into three indefinite layers i.e. layers 9, 11, and 13. The fibres of the network are stained faintly, but are more evident ventrally and laterally than dorsally where they are very indistinct and indefinite. Peripherally the network is continuous with the fibres of layer 8 and centrally with similar network of layer 14. Ventrally it is continuous with the network of the tegmental gray including the oculomotor and the trochlear nuclei and also of the torus semicircularis. Rostrally, however, the network probably is continuous with its fellow of the opposite side through the posterior commissure.

Layer 14:

This layer, too, consists of a plexiform network of fibres which resembles that of the previous layers. In fact, it is very probable that both the network of fibres of this and the previous layers belong to the stratum fibrosum periventriculare.

Layer 15:

No fibres are visible in this layer.

Silver preparations./

Silver preparations

In these preparations, in contrast to the iron-haematoxylin ones, the fibres show very distinctly and to a greater extent in all the layers of the optic tectum, particularly in the layers, 2, 4, 6, 8, 12 and 14.

Layer 1:

It consists of a network of fibres which merges dorsally and ventrally with the tractus opticus marginalis pars medialis and tractus opticus marginalis pars lateralis respectively. Some of the radial fibres from the deeper zones can be seen to enter this layer.

Layer 2:

This layer resembles layer 1, but is much narrower than the latter and its network is more compact. Otherwise the arrangement and distribution of its fibres are exactly the same as in the previous layer, and, in fact, are probably also optic in nature.

Layers 3 to 6:

The stratum fibrosum et griseum superficiale has been so called since it constitutes a broad zone consisting of alternate cell and fibre layers. Layers 3 and 5 belong /

belong to the cell layers, while 4 and 6, to the fibre layers respectively. In view of the description of the optic tectum in lizards by Huber and Crosby ('33) these layers can further be called:

(i) stratum griseum superficiale superficiale (or, layer 3)

(ii) stratum fibrosum superficiale superficiale (or, layer 4)

(iii) stratum griseum superficiale profundum (or, layer 5)

(iv) stratum fibrosum superficiale profundum (or, layer 6)

Besides the scanty cells and nuclei layers 3 and 5 consist of fibres of all kinds - transverse, oblique and radial, cut into different lengths, and arranged in a plexiform manner. The radial and the oblique fibres form the characteristic feature of the layers.

The transverse fibres, on the other hand, predominate in layers 4 and 6 being especially marked again in the ventral half of the layers. Each layer is a compact network of fibres resembling layer 2, and is probably also chiefly optic in nature. The network of layer 6, however, throughout its extent, is more marked than that of layer 4. Moreover,/

Moreover, some of the fibres decussate dorsally in the roof of the optic tectum, while ventrally they enter the tegmentum.

The radial fibres, appearly singly, permeate all the layers and are continuous peripherally with layer 2, and centrally with layer 7.

Layer 7:

All types of fibres - transvers e, oblique, and radial - are present in this layer. The fibres are arranged in a plexiform manner through the scattered cells and nuclei of the layer. The transverse and oblique fibres appear in small bundles and merge with those of layer 8. The radial fibres enter the superficial as well as the deeper layers.

Layer 8:

This layer, too, consists of transverse, oblique and radial fibres. The fibres show more distinctly in these preparations than in the iron-haematoxylin ones. The transverse and oblique fibres outnumber the radial and constitute the characteristic feature of this layer. They appear in small compact bundles of different lengths extending even into layer 7. Dorsally and rostrally they decussate /

decussate in the dorsal part of the posterior commissure (Fig. 13); further caudally they do so in the decussatio tecti mesencephali (Fig. 10). Ventrally they enter the tegmentum forming the dorsal and the ventral tecto-bulbar and tecto-tegmental tracts and decussate in the dorsal and the ventral tegmental decussations (Figs. 14, 15). Besides they enter the torus semicircularis, oculomotor nucleus, and nucleus isthmi of the same side. Further they establish communication with the fasciculus longitudinalis medialis.

The radial fibres are very few in number and appear singly. Peripherally they enter the superficial layers, described already, and centrally they join the plexiform network of the deeper periventricular layer.

Layers 9 to 13:

The plexiform network of fine fibres, contained in these layers, is aggregated into two very narrow zones i.e. layers 10 and 12, which demarcate the entire cellular and nuclear zone into three indefinite layers i.e. layers 9, 11, and 13, described already. Peripherally the network is invaded by the radial fibres of layer 8, and is continuous centrally with the network of layer 14. Dorsally it is continuous with its fellow of the opposite side/

side through the dorsal part of the posterior commissure rostrally and the roof of the optic tectum caudally. Ventrally, however, it enters the tegmentum and is continuous with the network of the torus semicircularis (Fig. 10).

Layer 14:

This layer resembles layers 10 and 12.

Layer 15:

No fibre is present in this layer.

B. TORUS SEMICIRCULARIS.

The torus semicircularis, as already stated, lies in the floor of the optic ventricle. It forms a prominent bulging of the medial part of the floor of the ventricle at the level of the oculomotor nucleus (Fig. 14). Opposite the caudal part of this nucleus it fuses in the median plane with its fellow of the opposite side separating completely the optic ventricle from the aqueduct. The fused tori thus form the roof of the aqueduct. The optic ventricle, however, does not extend to the caudal limit of the torus, but stops short a little caudal to the site/

site of fusion of the two tori. Throughout its entire rostro-caudal extent it lies under cover of the optic tectum.

Carbol-fuchsin preparations.

The torus semicircularis rostral to the site of fusion contains a nuclear mass, which, in transverse section, appears to be oval in shape with its long axis transverse. The nucleus consists of (i) a peripheral capsular zone, and (ii) a central area (Fig. 9).

The peripheral capsular zone consists of 4 to 5 rows of closely packed cells and nuclei, which are continuous dorso-laterally with those of the stratum griseum periventriculare of the optic tectum. It is, however, deficient ventro-laterally. The cells and nuclei of the central area are scattered diffusely and arranged in small groups. Laterally through the deficient part of the capsule they are continuous with those of the outer part of the stratum griseum periventriculare and the more superficial layers of the optic tectum (Fig. 9). The cells and nuclei of both zones correspond with those of the optic tectum.

Caudal to the site of fusion of the tori the central part/

part gradually becomes completely fused with its fellow of the opposite side. The peripheral capsular zone, on the other hand, which can still be seen just caudal to the site of fusion, gradually becomes indefinite being almost completely lost further caudally (Fig. 12). At this level the periventricular gray of the torus fuses with that of the optic tectum, and forms a dorsal cap for the fused central mass, which is continuous laterally on each side with the more superficial layers of the optic tectum.

Iron-haematoxylin preparations.

The central area of the nucleus consists of a network of fine fibres. The fibre density is greater in the lateral than in the medial part of the nucleus.

Dorso-laterally the network is directly continuous with the similar network of the stratum griseum periventriculare and the transverse fibres of the stratum album centrale of the optic tectum. Ventro-laterally, however, it is continuous with a myelinated fibre tract of the tegmentum which lies on the medial aspect of the tecto-bulbar tract.

Medially, caudal to the fusion of the tori, the network is directly continuous with its fellow of the opposite side./

side.

Silver preparations

These preparations, unlike the previous ones, present a denser network of fine fibres, the fibre density being a little greater ventrally and laterally. Otherwise the description given above for the myelinated fibres also applies to these preparations (Figs.10,13,14).

REVIEW OF THE OBSERVATIONS

1. The optic lobes are two in number and are situated one on each side of the middle line. They are very well developed being smaller than the cerebrum, but larger than the cerebellum. The relative size of the different parts of the brain is also evident from the photographs.
2. The lobes are fused medially, a median longitudinal sulcus intervening between them dorsally. Each lobe is encircled by a sulcus, the sulcus limitans optici, /

optici, which demarcates the lobes from the surrounding parts.

3. Anteriorly the lobes are separated from the cerebrum by the diencephalon and posteriorly from the cerebellum by a cleft.

4. Each lobe contains a cavity, called the optic ventricle. Medially the cavity communicates with its fellow of the opposite side and also with the aqueduct. The optic ventricle divides the lobe into a roof, the optic tectum, and a floor, the torus semicircularis, which merges with the tegmentum. The lateral recess of the ventricle demarcates the roof from the floor laterally and does not correspond to the sulcus limitans of the aqueduct.

The two tori semicirculares fuse with each other in the median plane at the caudal part of the oculomotor nucleus and form the roof of the aqueduct separating the latter completely from the optic ventricle.

The optic ventricle does not extend up to the caudal limit of the optic tectum, but stops short a little behind the site of fusion of the tori semicirculares.

5./

5. The torus semicircularis throughout its rostro-caudal extent lies under cover of the optic tectum and, unlike that of the lizard, does not come to the surface caudal to the tectum.

6. Optic tectum:

(A) Fifteen layers have been observed from histological studies. The layers have been named from without inwards. The lamination of the more superficial layers (i.e. 1 to 6) is very indefinite in the Nissl preparations. The stratum fibrosum et griseum superficiale consists of four alternate cell and fibre layers. The stratum griseum centrale is a well defined broad zone lying superficial to the stratum album centrale, while the stratum griseum periventriculare presents only five (3 cell and 2 fibre) layers. The stratum fibrosum periventriculare is a narrow zone of plexiform network of fine fibres.

(B) Cyto-architecture:

(a) The layers consist chiefly of round and oval nuclei without apparent cytoplasm containing single or multiple particles. Some of these nuclei are a little larger than the others. Indefinite/

definite cytoplasmic differentiation in relation to some of these nuclei suggests that they belong mostly to the pyramidal type of cells. A few small and large stellate cells are also present here and there.

Some fusiform nuclei are scattered through all the layers and probably belong to the blood vessels.

(b) The cells and nuclei are mostly aggregated in the periventricular layers. In the more superficial zones i.e. layers 1 to 8 they are very scanty and diffuse and the differentiation of the layers is very difficult and indefinite.

(c) The periventricular cells and nuclei are further differentiated into three indefinite zones i.e. layers 9, 11, and 13 by two narrow zones of plexiform network of fibres, layers 10 and 12. Ventrally they are continuous with the neurons of the tegmentum and the torus semicircularis. Some of these cells and nuclei even adhere to the ependymal layer.

(d) The subcommissural organ appears as a thickening of the ependymal layer produced by an aggregation of the ependymal nuclei in the roof of the ventricle in the median plane deep to the posterior commissure.

(e) The mesencephalic neurons of the trigeminal nerve, unlike those of the lizard, are situated more rostrally and centrally. They appear as large isolated round, or piriform cells situated mainly amidst the cells and nuclei of layers 13 and 15. They are present only at the level of the posterior commissure and disappear entirely further caudally.

(C) Fibro-architecture:

(a) The myelinated fibres of layers 1, 2, 4, and 6 merge dorsally and ventrally with the tractus opticus marginalis pars medialis and tractus opticus marginalis pars lateralis respectively and are probably optic in nature.

(b) The transverse fibres in layer 8 appear in small compact bundles extending peripherally even into layer 7. Dorsally they decussate in the dorsal part of the posterior commissure rostrally and commissura tecti mesencephali further caudally. Ventrally they constitute the different tecto-bulbar tracts and decussate ultimately in the tegmental decussations.

The /

The myelinated fibres of layer 8 constitute the most characteristic feature of the optic tectum in iron-haematoxylin preparations having the greatest density of staining and the thickest myelin sheaths.

(c) The plexiform network of layers 10, 12, and 14 predominantly consists of relatively thinly myelinated or non-myelinated fibres.

(d) The radial fibres extend through all the layers of the optic tectum.

(e) The optic tectum is also very intimately connected with the torus semicircularis of the same side.

7. Torus semicircularis

(A) Cyto-architecture:

(a) It consists of an oval nucleus the long axis of which is transverse in transverse section. The nucleus presents:

(i) a peripheral capsular zone, and

(ii) a central area.

(i) The capsular zone consists of 4 to 5 rows of closely packed cells and nuclei, which are continuous with those of the stratum griseum periventriculare of the optic tectum. It is deficient, however, ventro-laterally.

(ii) The central area, on the other hand, presents very loosely scattered cells and nuclei, which are arranged also in small groups. It merges with the superficial layers of the optic tectum (i.e. layers 1 to 8), and with its fellow of the opposite side as well caudal to the site of fusion of the two tori semicirculares.

(B) /

(B) Fibro-architecture:

(a) The nuclear mass contains a network of fine fibres in which the non-myelinated fibres and fibres not demonstrable with iron haematoxylin markedly predominate. The network is denser laterally.

(b) The network is intimately connected with its fellow of the opposite side and with the optic tectum of the same side by the transverse fibres of layer 8 and by periventricular fibres.

(c) Ventrally and laterally it is connected with the fibres of the lateral lemniscus.

Class - Reptilia.

Sub-class - Diapsida.

Order - Squamata.

Sub-order - Lacertilia.

Species - Lacerta viridis
(green lizard)
(Age - Adult).

MEASUREMENTS.

I. (a) Length of lizard - 30.0 cm.

(b) " " brain - 1.2 cm.

II. (a) Weight of lizard - 17.0 gm.

(b) " " brain - 0.13 gm.

III. Optic lobe:

(a) Antero-posterior - 0.24 cm.

(b) Transverse - 0.3 cm.

(c) Supero-inferior - 0.35 cm.

IV. Cerebrum:

(a) Antero-posterior - 0.6 cm.

(b) Transverse - 0.2 cm.

(c) Supero-inferior - 0.35 cm.

MACROSCOPIC OBSERVATIONS.

The optic lobes are two in number. Each lobe is more or less oval in shape. Each measures 2.5 mm. antero-posteriorly, 3.0 mm. transversely and 3.5 mm. vertically. The lobes are placed obliquely, their longitudinal axes being directed, from above, downward, forward, and outward. Dorsally the lobes are apposed against each other, a deep median/

median fissure intervening between them. Ventrally the fissure extends up to the roof of the ventricle. Medially the lobes are fused with each other dorsally to form the roof of the ventricle while ventrally they fuse with the diencephalon, tegmentum of mesencephalon, and the rostral part of rhombencephalon from before backward. A circular sulcus, the sulcus limitans optici, encircles each lobe. The sulcus is most marked ventrally and caudally and demarcates each lobe from the surrounding parts. The lower end of each lobe is narrower than the upper and is related ventrally to the trochlear nerve. Each lobe is slightly overlapped by the cerebrum rostrally and cerebellum caudally (Fig. 16).

Dorsally each lobe presents an irregular rectangular superior surface, the lateral border of which is a little longer than the medial. The surface is traversed by a shallow antero-posterior groove. The anterior surface is flat and lies in contact with the corresponding posterior surface of the respective cerebral hemisphere, a deep fissure intervening between them. The slightly convex posterior surface is covered and partially overlapped by the corresponding concave anterior surface of the cerebellum. The lateral surface is convex in all directions. Both/

Both the lateral and the superior surfaces are free and covered by a thin pigmented membrane, the pia mater.

The optic lobe is well developed in this form being a little smaller than the cerebrum, but much bigger than the cerebellum. The large size of the lobe is also evident in the photographs, and has been accounted for by the increased acuity of vision and the big size of the eyeball (Fig. 16).

Each lobe contains a cavity, called the optic ventricle, which is, in fact, the lateral extension of the aqueduct. Each ventricle communicates supero-medially with the aqueduct of the mesencephalon and with its fellow of the opposite side as well. The ventricle divides each lobe into a roof, the optic tectum, and a floor, the torus semicircularis, which merges with the tegmentum of the mesencephalon (Fig. 17). The lateral recess limits the lateral extent of the ventricle and does not indicate the position of the sulcus limitans of the aqueduct, which is represented by a groove on the wall of the aqueduct ventral to the torus semicircularis (Fig. 18). There is also an upward extension of the ventricle into the roof, called the superior recess.

The tectum extends from the level of the posterior commissure/

commissure rostrally to the emergence of the trochlear nerve through the medullary velum caudally.

MICROSCOPIC OBSERVATIONS.

A. OPTIC TECTUM.

The optic tectum in reptiles has been the subject for experimental and histological studies by different workers especially in its relation to vision and optic pathways. All the previous workers noticed the stratification of the optic tectum - some (P. Ramón, '96; de Lange, '13; Huber and Crosby, '26) described the different layers on a histological basis, while others (Bellonci, '88; Cairney, '26; Huber and Crosby, '33, '33a, and '34; Armstrong, '50) did that entirely on a functional basis. The following table will give an idea about the total number of layers of the optic tectum, worked out by different workers from time to time:

Serial/

Serial number	Name of workers	Year of the work	Subject of work	Number of layers
1	Bellonci	1888	Emys	8
2	P. Ramón	1896	Lacerta agilis	14
3	de Lange	1913	"	"
4	Huber & Crosby	1926	Alligator	"
5	Cairney	1926	Sphenodon	5
6	Huber & Crosby	1933	Various reptilian tecta	6
7	Armstrong	1950	Lacerta vivipara	7

The author, working exclusively on the morphology and histology of Lacerta viridis, has observed 16 layers in the optic tectum including the ependymal layer. Functionally, however, all these layers can easily be reduced to the 8 layers of Bellonci ('88), the 6 layers of Huber & Crosby ('33), or the 7 layers of Armstrong ('50). The latter workers (Huber and Crosby, and Armstrong) excluded, however, the ependymal layer from their classification. In table 3 the different layers, observed by the author, have been correlated with those of the other workers.

Table 3./

Table 3. Comparison of the author's classification of the layers of the optic tectum with that of other workers.

Number of layers	Author's Observations	Armstrong ('50)	Huber & Crosby ('33, '33a, '34)	Cairney ('26)	P. Ramón ('96) de Lange ('13) Huber & Crosby ('26)	Bellonci ('88)
1	Stratum zonale (St.z.)	(1) → 'Do'	-	-	-	Layer 8
2	Stratum opticum (St.o.)	(2) → 'Do'	(1) → 'Do'	(e)	Layer 14	Layer 7
3	Cell layer	Stratum fibrosum et griseum superficiale (St.f.g.s.)			Layers 8-9-10-11-12-& 13.	
4	Fibre layer					
5	Cell layer	(3)	(2)			Layer 6
6	Fibre layer			(d)		
7	Cell layer					
8	Stratum griseum centrale (St.g.c.)	(4) → 'Do'	(3) → 'Do'		Layer 7	Layer 5 or 6

9/

Table 3. (Cont'd.)

Number of layers	Author's Observations	Armstrong ('50)	Huber & Crosby ('33, '33a, '34)	Cairney ('26)	P. Ramón ('96) de Lange ('13) Huber & Crosby ('26)	Bellonci ('88)
9	Stratum album centrale (St.a.c.)	(5) 'Do'	(4) 'Do'	(c)	Layer 6	Layer 5
10	Outer granular layer	Stratum griseum periventriculare (St.g.p.)			Layers 3 - 4 - 5	Layers 3 & 4
11	Outer plexiform layer					
12	Middle granular layer		(5) 'Do'	(b)		
13	Inner plexiform layer	(6) Stratum griseum periventriculare				
14	Inner granular layer					
15	Stratum fibrosum periventriculare (St.f.p.)	(7) 'Do'	(6) 'Do'	(a)	Layer 2	Layer 2
16	Stratum ependymale (St.e.)	-	-	-	Layer 1	Layer 1

Carbol-fuchsin preparations (Figs.17,18,19)

Layers 1 to 7:

Small round and oval nuclei without any apparent cytoplasm lie diffusely scattered throughout these layers. Their number is greater in layer 4 and they border layer 6; this is also evident from the iron-haematoxylin and silver preparations. The nuclei are usually of two types - some contain multiple distinct particles while others have only one, probably the nucleolus. The cells chiefly belong to the small stellate type containing few Nissl granules. A few relatively large stellate cells containing multiple Nissl granules lie scattered here and there particularly in layers 4, 5, and 6. A few pyramidal and fusiform cells are also present.

Dorso-medially along the roof of the ventricle the cells and nuclei of all these layers are continuous with those of the opposite side. Ventrally, however, they become scattered and gradually merge with those of the tegmentum. A number of capillaries of blood vessels with their pial extensions enter the optic tectum from the surface, and traverse its entire thickness.

Layer 8:

This is the broadest layer of the optic tectum. The cells /

cells and nuclei are like those of the previous layers, and are scattered irregularly with distinct intercellular spaces between them.

Dorsally towards the median plane the layer becomes a little narrower and is continuous along the roof of the ventricle with that of the opposite side. Ventrally it stops suddenly and is limited by a zone, relatively clearer and free from nuclei, corresponding in iron-haematoxylin and silver preparations, to the ventral tecto-bulbar fibres.

Layer 9:

This is a relatively clearer zone containing only a few scattered nuclei and cells, as in the previous layers. The layer is narrower dorsally gradually becoming broader ventrally. A few small stellate and pyramidal cells lie scattered throughout the layer, and a few large stellate cells are also present especially ventrally.

Dorso-medially the layer is continuous with its fellow of the opposite side along the roof of the ventricle, while ventro-medially it merges with the tegmentum.

Layers 10 to 14:

This is a fairly broad zone consisting of more closely packed nuclei and cells. The nuclei and cells re-

semble/

semble those of the previous layers and according to their mode of distribution have been differentiated into three indefinite layers - outer granular layer, or layer 10, middle granular layer, or layer 12, and inner granular layer, or layer 14, by two relatively clear zones - outer plexiform layer or layer 11 and inner plexiform layer or layer 13.

The outer granular layer consists of 4 to 5 rows of nuclei and cells while the middle layer presents only 1 to 2 or even 3 rows. Differentiation of these two layers is very difficult especially laterally and ventrally. The inner granular layer, on the other hand, is the narrowest of all the three and consists chiefly of one row of cells and nuclei, but, at places, becomes even 2 rows thick. Dorso-medially all the granular layers converge in the roof of the ventricle and are continuous with those of the opposite side. Ventrally, however, they merge with the torus semicircularis and the tegmentum.

A few large round and piriform cells are scattered especially dorsally amidst the cells and nuclei of layers 10, 12, and 14, predominating particularly in layers 10 and 12. These are the mesencephalic neurons of the trigeminal nerve. They extend from the level of the caudal/

caudal part of the posterior commissure to the most rostral part of the trochlear nucleus. They appear singly, contain multiple Nissl granules, and are more deeply stained.

The subcommissural organ appears as a thickening of the ependymal layer and lies deep to the posterior commissure throughout its rostro-caudal extent.

Layer 15:

This is another relatively clear zone and resembles layers 11 and 13. A few cells and nuclei are scattered here and there. Along the roof the layer is continuous with its fellow of the opposite side dorsally. Ventromedially, however, it merges with a similar layer of the floor of the ventricle.

Layer 16:

This layer is formed by 1 to 3 rows of round and of oval nuclei with their long axes set at right angles to the ventricular surface. The round nuclei resemble those of the previous layers.

Iron-haematoxylin preparations (Fig. 21).

Layer 1:

This layer shows no myelinated fibres.

Layer 2:/

Layer 2:

There are a few bands of distinctly stained fibres, cut into short lengths. The fibre bands are for the most part distributed transversely, i.e. parallel to the surface, on the lateral and ventral aspect of the lobe. Dorsal and dorso-medial to the optic ventricle this layer shows cross-sections of fibres arranged in groups. Dorso-medially and ventro-laterally the layer merges with tractus opticus marginalis pars medialis and tractus opticus marginalis pars lateralis respectively. At places, particularly laterally, a few short oblique fibres can also be found, some of which are seen to take an inward course. Besides, a few short radial fibres are also present here and there.

Layers 3 to 7:

This is a very broad zone comprised of alternate cell and fibre layers.

Layer 3 is a relatively clear zone consisting of a few transverse, oblique, and radial fibres, cut into short lengths. The transverse fibres predominate ventro-laterally and merge with layers 2 and 4 here and there.

Layer 4 is a relatively broader zone being about 4 to 5 times as broad as layer 2. The fibre density is minimum/

minimum laterally, but increases a little both dorsally and ventro-laterally. The arrangement and distribution of the fibres resemble those of layer 2 and are, in fact, optic in nature. The radial fibres, few in number, are scattered here and there.

Layer 5 is a little broader than layer 4 and is more or less of uniform thickness throughout its distribution. It consists of very few irregularly scattered fibres, cut into very short lengths, and is traversed by some faintly stained radial fibres as well.

Layer 6 is as broad as layer 4, but the fibres here are more loosely scattered instead of being in definite bundles. The depth of staining of the fibres is almost like those of layers 2 and 4. Besides the transverse and cross section of fibres the layer presents some oblique and radial fibres as well. Dorsally the layer is continuous with its fellow of the opposite side. Ventrally the distribution of the transverse fibres resembles that of layers 2 and 4.

Layer 7 is a relatively clearer zone consisting of radial, transverse, and oblique fibres. The fibres are very loosely scattered except ventro-laterally where the transverse and the oblique fibres predominate and are arranged/

arranged in more or less compact bundles. The radial and the rest of the transverse and oblique fibres are thin and are stained very faintly. Dorsally the layer is continuous with its fellow of the opposite side. The radial fibres enter the superficial as well as the deeper layers.

Layer 8:

This is chiefly a broad cellular zone but contains both transverse and radial fibres. The transverse fibres, cut into short lengths, appear in compact bundles, and are arranged in parallel laminae, which radiate outward at right angles to the wall of the optic ventricle. Each of the laminae is thinnest towards the surface of the optic tectum, where the fibre bundles are smaller and less compact. This thinning of the laminae towards the surface accentuates the slight divergence of the laminae in this direction. These laminae of fibres merge with the subjacent deeper layer i.e. layer 9.

The radial fibres appear singly and lie within the transverse fibre laminae and in the intervals between them as well. They are continuous with similar fibres of the more superficial as well as of the deeper layers.

Dorsally/

Dorsally along the roof of the ventricle the layer seems to merge with its fellow of the opposite side.

Layer 9:

This layer is most conspicuous because of the presence of very thick and deeply stained myelinated fibres. It is narrower dorsally becoming gradually broader ventrally. Like the previous layer this layer, too, consists of both transverse and radial fibres. The mode of arrangement and distribution of the fibres resembles that of the previous layer (layer 8) except that the transverse fibres outnumber the radial ones and constitute the most characteristic feature of the layer.

Rostrally the transverse fibres are continuous with those of the opposite side through the dorsal part of the posterior commissure. Further caudally they do so along the roof of the ventricle forming the commissura tecti mesencephali. Ventrally they constitute the dorsal, intermediate, and ventral tecto-bulbar tracts, by which they enter the tegmentum and come into relationship with the different tegmental neurons of the mesencephalon of the same side - oculomotor nucleus, red nucleus, substantia nigra, /

nigra, and nucleus isthmi. Besides, the dorsal and the ventral tecto-bulbar tracts cross to the opposite side decussating in the median plane forming the commissura tecto-bulbaris dorsalis cruciatus and commissura tecto-bulbaris ventralis cruciatus respectively. Through these commissures the dorsal and the ventral tecto-bulbar tracts possibly establish communications with the tegmental neurons of the opposite side as well. No direct connection of these fibres with the trochlear nucleus can, however, be noticed. Fibres of the dorsal tecto-bulbar tract, on the contrary, are very intimately connected with the fasciculus longitudinalis medialis, which probably indirectly connects the optic tectum with both the oculomotor as well as the trochlear nuclei. In addition to these distributions the dorsal tecto-bulbar tract also comes into relation with the neurons of the torus semicircularis of the same side. The radial fibres, usually appearing singly, enter the superficial and the deeper layers.

Layers 10 to 14:

These layers consist of a plexiform network of very fine fibres. The network is very faintly stained and is more evident in layers 11 and 13.

It/

It is continuous peripherally with layer 9, especially with the radial fibres of the latter, and centrally with that of layer 15. Dorsally it is continuous with its fellow of the opposite side along the roof of the ventricle; ventrally it is connected with the network of the torus semicircularis.

Layer 15:

This layer resembles layers 11 and 13 and, like the latter, consists of very fine myelinated fibres, also stained faintly and arranged in a plexiform manner. Peripherally, as stated, the network is continuous with the similar network of the more superficial layers. Dorsally it is continuous along the roof of the ventricle with its fellow of the opposite side; ventro-medially it merges with a similar network of the floor of the ventricle and the tegmentum and is also connected with the network of the torus semicircularis. It appears from the above that the plexiform networks of this and of the previous layers, especially of layers 11 and 13, have the same character, disposition, and distribution of their fibres. Therefore, it is very probable that they are derived from the stratum fibrosum periventriculare.

Layer 16:

No/

No fibres are visible in this layer.

Silver preparations (Figs. 20, 22, 23)

The fibres of the different layers of the optic tectum show very distinctly and to a greater extent in these preparations than in the iron-haematoxylin ones. This is particularly true in the layers 1, 3, 5, 7, 11, 13, and 15. Thus it is evident that the non-myelinated fibres predominate markedly over the myelinated fibres, especially in the layers mentioned already.

Layers 1 and 2:

Both the layers consist chiefly of transverse fibres, cut into different lengths and arranged into irregular bundles. The fibres of layer 1 are more closely packed than those of layer 2. Ventrally the layers become a little broader, the fibres being distributed mostly obliquely. Dorso-medially and ventro-laterally the layers merge with tractus opticus marginalis pars medialis and tractus opticus marginalis pars lateralis respectively. These fibres belong probably to the marginal optic tract. The radial fibres enter the layers from the deeper zones, some extending as far as the surface of the optic tectum.

Layers 3 to 7:

In /

In these preparations, unlike the iron-haematoxylin ones, the differentiation of the layers is not very definite.

Layers 3, 4, 5, and 6 consist of both radial and transverse fibres which have been cut into different lengths. In layer 3 the transverse fibres predominate and are very loosely scattered. In layer 4 the transverse fibres again form the most marked feature and are arranged into more compact bundles. In layer 5, which is relatively broader than layer 3 or 4, the radial fibres stand out most prominent, a fair number of isolated transverse fibres being also present here and there. Layer 6, however, is not very well defined. It presents a few bundles of compact fibres and is bordered by the rounded nuclei which are diffusely scattered within the layer as well. Layer 7 contains a network of radial and transverse fibres. The radial fibres are continued into the subjacent layer 8 and transverse fibres are also represented here. Ventro-laterally the transverse fibres have the same mode of distribution as those of layer 2 and are probably also optic in nature belonging to the tractus opticus marginalis pars lateralis. Some of the transverse fibres, particularly of layers 6 and 7, bend medially on the ventral aspect of the ventricle. Dorso-medially along the roof of the ventricle all the layers /

layers converge and are continuous with those of the opposite side. The radial fibres, continuous with those of superficial and deeper layers, are thicker centrally and thinner peripherally.

Layer 8:

The scattered nuclei and cells of this layer are traversed by both transverse and radial fibres, cut into different lengths and arranged in a plexiform network. The transverse fibres, cut into very short lengths and appearing in compact parallel bundles, are arranged in parallel laminae radiating outward at right angles to the wall of the ventricle. Centrally these laminae are a little broader and merge with those of the deeper layer or layer 9. Ventrally they have the same mode of distribution as those of layer 9. Dorso-medially along the roof of the ventricle the layer merges with its fellow of the opposite side. The radial fibres, as in iron-haematoxylin preparations, appear singly being thicker centrally and thinner peripherally; they enter both the superficial and the deeper layers.

Layer 9 /

Layer 9:

The layer is narrower dorsally but gradually becomes broader ventrally. Like the previous layers this layer too, consists of transverse and radial fibres. The transverse fibres, having the same arrangement and distribution like those of layer 8, form the most characteristic feature of this layer. The parallel laminae of fibres are relatively thicker centrally. Dorso-medially along the roof of the ventricle the fibres decussate with those of the opposite side giving rise to decussatio tecti mesencephali. More rostrally, however, they do so in the dorsal part of the posterior commissure (Fig.20). Ventrally they bend medially to enter the tegmentum of the mesencephalon forming the tecto-tegmental and tecto-bulbar tracts. Rostro-caudally the tecto-bulbar tract can, however, be differentiated into 3 parts - dorsal, intermediate, and ventral. The fibres of the dorsal and ventral tecto-bulbar tracts decussate successively in the median plane of the tegmentum of the mesencephalon forming the dorsal and the ventral tegmental decussations respectively, or the decussatio tecto-bulbaris dorsalis cruciatus and decussatio

tecto /

tecto-bulbaris ventralis cruciatus. By fibres of these tracts, as already stated in the iron-haematoxylin preparations, the optic tectum comes into relationship with the different tegmental neurons of the mesencephalon - oculomotor nucleus, red nucleus, and substantia nigra of the same as well as of the opposite side. The fibres of the dorsal tecto-bulbar tract, further are directly connected with the fasciculus longitudinalis medialis, which probably indirectly correlates the optic tectum with the oculomotor and the trochlear nuclei. They are also very closely related with the aggregated neurons of the torus semicircularis of the same side. The fibres of the ventral tecto-bulbar tract, on the other hand, are related with the homo-lateral nucleus isthmi caudally.

The radial fibres, appearing singly and coursing within and in between the parallel laminae of fibres, enter /

enter the superficial as well as the deeper layers.

Layers 10 to 14:

All these layers, taken together, constitute the broad zone of the stratum griseum periventriculare, which is indefinitely differentiated into 3 granular layers i.e. layers 10, 12, and 14 by two very narrow zones of fine plexiform fibres, layers 11 and 13. The plexiform networks of layers 11 and 13 are continuous with each other through layer 12. Peripherally the network of layer 11 is continuous with some of the radial fibres of the more superficial layers, while centrally the network of layer 13 is continuous with the similar network of layer 15. Rostrally the networks are continuous with their fellows of the opposite side through the posterior commissure. Further caudally, however, they do so along the roof of the ventricle. Ventrally they merge with the network of the torus semicircularis.

Layer 15:

This is another broad zone consisting of a plexiform network of very fine fibres. The network resembles layers 11 and 13 in character, arrangement, and disposition of its fibres. Peripherally, as stated previously, it is continuous with similar network of the superficial/

superficial layers. Dorsally it is continuous with its fellow of the opposite side through the posterior commissure rostrally and roof of the ventricle caudally. Ventrally, however, it merges with the tegmentum and is also continuous with the network of the torus semicircularis.

Layer 16:

This layer is entirely free from fibres and corroborates the observations of the carbol-fuchsin preparations in the arrangement of the nuclei.

B. TORUS SEMICIRCULARIS.

The torus semicircularis lies in the floor of the optic ventricle, and commences at the level where the latter communicates with its fellow of the opposite side and the aqueduct (Fig. 17). Caudally it gradually approaches the median plane bulging into the optic ventricle, which is reciprocally narrowed. The optic ventricle, unlike the frog, does not extend so far caudally, but stops short at the caudal part of the oculomotor nucleus. The two tori semicirculares meet each other in the median plane at the level of the rostral end/

end of the trochlear nucleus and undergo complete fusion forming the roof of the aqueduct (Fig. 18). The greater part of the torus semicircularis lies under cover of the optic tectum, but unlike the frog, its most caudal part is exposed on the surface like the mammalian inferior colliculus (Fig. 23).

Carbol-fuchsin preparations.

The torus consists of a peripheral capsular zone and a central area.

The peripheral capsular zone is incomplete ventrally and laterally (Fig. 19). It is, however, completely absent caudally where the two tori fuse with each other completely (Fig. 18).

It consists of a few rows of cells and nuclei without apparent cytoplasm which are arranged more compactly than the central area. The cells consist of the small stellate and pyramidal types. The nuclei are round and oval in shape containing single or multiple distinct particles. Some of the nuclei are a little larger than the rest. Besides these a few fusiform cells can also be seen scattered here and there. Dorso-laterally the zone is continuous with the inner periventricular layer of/

of the stratum griseum periventriculare of the optic tectum and ventrally with the periventricular layer of the tegmentum (Fig. 19).

The central area, on the other hand, consists of cells and nuclei, some of which are arranged in small groups, while others are scattered very diffusely. The cells belong mostly to the small stellate type including a few large stellate cells scattered here and there. A few pyramidal and fusiform cells are also present. The nuclei are like those described previously. Dorsolaterally it is continuous with the stratum griseum periventriculare and stratum album centrale of the optic tectum. Ventrally it merges with the tegmentum (Fig. 19). Medially, however, it is limited rostrally by the capsular cells, but further caudally it merges with its fellow of the opposite side (Fig. 18).

The cells of the mesencephalic nucleus of the trigeminal nerve extend caudally to the level of the rostral part of the trochlear nucleus. Here they lie near the median plane amongst the periventricular cells of the optic tectum dorsal to the capsular zone of the central nuclear mass.

Iron-haematoxylin preparations./

Iron-haematoxylin preparations.

The central area consists of a network of fine myelinated fibres the density of which is greater ventro-laterally.

Dorso-laterally the network is continuous with that of the stratum griseum periventriculare of the optic tectum, and is in continuity with the fibres of the dorsal tecto-bulbar tract. Laterally it is continuous with the radial fibres of the stratum album centrale of the optic tectum and ventrally with a similar network of the peri-ventricular gray of the tegmentum.

Ventro-laterally at the level of the trochlear nucleus fibres of the octavo-mesencephalic tract can be seen to enter it. It is also connected with a similar network of fibres of the nucleus isthmi of the same side, but no connection can be found in these preparations with its fellow of the opposite side.

At the level of the trochlear nucleus caudally the mesencephalic roots of the trigeminal nerve can be seen to course along the dorso-lateral aspect of the peripheral part of this area.

Silver preparations (Figs. 20, 22, 23).

These/

These preparations, too, present a network of very fine fibres, the number and density of which are much greater than in the iron-haematoxylin ones. It is thus evident that the non-myelinated fibres predominate markedly over the myelinated.

The arrangement and distribution of the fibres, however, are the same as in the iron-haematoxylin preparations except that caudally the two tori semicirculares are connected very densely by unmyelinated fibres.

REVIEW OF THE OBSERVATIONS.

1. The optic lobes are very well developed in this form. Their large sizes and relative proportions in respect to the cerebrum and the cerebellum are quite evident in the photographs. They are fused in the median plane, a deep longitudinal sulcus intervening between them dorsally.
2. The lobes are partially overlapped by the cerebrum anteriorly and the cerebellum posteriorly. Each lobe is smaller than the cerebrum, which presents a smooth surface having no convolutions. It is larger than the cerebellum, which is very poorly developed/

developed and presents a smooth surface.

3. Each lobe is encircled by a circular sulcus, the sulcus limitans optici, which demarcates the lobe from the surrounding parts.

4. The optic ventricle, contained in each lobe, is very wide and divides the lobe into a dorsal thin walled roof, the optic tectum, and a ventral relatively thicker floor, the torus semicircularis, which, in its turn, is continuous with the tegmentum of the mesencephalon. The lateral recess of the ventricle demarcates the two parts. Supero-medially each ventricle communicates with the aqueduct and also with its fellow of the opposite side. In fact, it is the lateral extension of the aqueduct.

5. Like the frog, the two tori semicirculares undergo fusion in the median plane at the rostral level of the trochlear nucleus; but, unlike the frog, they do not separate the aqueduct from the ventricle. The fused tori form the roof of the aqueduct.

6. At the caudal limit of the optic tectum the fused tori semicirculares make their appearance on the surface and are the forerunner of the mammalian inferior colliculi.

7./

7. Optic tectum.

(A) From histological observations 16 layers have been described and named from without inwards. The different layers have been correlated with those of other workers in table 3. The lamination is more pronounced and definite in this form than in the frog. The stratum fibrosum et griseum superficiale shows five alternate cell and fibre layers, while the stratum griseum periventriculare presents only five layers.

(B) Cyto-architecture.

(a) Round and oval nuclei without apparent cytoplasm and containing single or multiple particles form the chief constituents of the optic tectum.

(b) The cells consist of the following types:

(i) stellate (small and large),

(ii) pyramidal, and

(iii) fusiform.

The small stellate cells constitute the greatest number and predominate markedly over others, which are few in number and lie scattered here and there.

(c)/

(c) There are very few or no cells or nuclei in the peripheral zone of the ependymal layer.

(d) The number of cells and nuclei in the stratum griseum periventriculare is fairly high. The cells and nuclei, as in the frog, appear in three layers of increasing density from within outwards.

(e) The stratum griseum centrale constitutes the broadest layer of cells and nuclei which are scattered diffusely having well spaced intervals between them.

(f) The cells and nuclei in the stratum fibrosum et griseum superficiale are also scattered very diffusely; but still they are aggregated in the form of definite layers. The differentiation of this broad zone into different layers is more pronounced in this form than in the frog.

(g) The mesencephalic neurons of the trigeminal nerve appear as large round or piriform cells scattered dorsally amidst the cells and nuclei of the stratum griseum periventriculare, especially in layers 10 and 12. They extend from/

from the caudal level of the posterior commissure to the rostral level of the trochlear nucleus.

(h) The subcommissural organ lies at the level of the posterior commissure and is formed by thickening of the ependymal layer by proliferation of its nuclei in the median plane of the roof of the ventricle. It is so called as it lies deep to the commissure.

(C) Fibro-architecture.

(a) Non-myelinated fibres, including fibres too thinly myelinated to stain with iron haematoxylin, predominate relatively to the myelinated fibres, especially in layers 1, 3, 5, 7, 11, 13, and 15.

(b) The myelinated fibres of layers 1, 2, 4, and 6, having the same mode of arrangement and distribution, seem to merge dorsally and ventrally with the tractus opticus marginalis pars medialis and tractus opticus marginalis pars lateralis respectively and are probably optic in nature.

(c) The transverse fibres of layer 9 are densely myelinated /

myelinated and form the most conspicuous feature of the optic tectum.
They decussate dorsally in the posterior commissure and the commissura tecti mesencephali. Ventrally they form the tecto-tegmental and the tecto-bulbar tracts and decussate further in the dorsal and the ventral tegmental decussations.

(d) The fibres of the periventricular plexus of fibres are very fine in character. Dorsally the plexus is continuous to the opposite side through the posterior commissure and the roof of the ventricle. Ventrally it merges with the tegmentum. Peripherally it is connected with the more superficial layers of the optic tectum.

(e) The radial fibres to a greater extent are non-myelinated and traverse all the layers of the optic tectum.

8. Torus Semicircularis

(A) Cyto-architecture.

(a) It consists of two parts - peripheral capsular and central.

(b) The peripheral capsular zone is deficient ventrally and laterally, and consists of more compact cells and nuclei, which are continuous with /

with the tegmentum and, especially, with the inner granular layer of the stratum griseum periventriculare of the optic tectum. The cells are of the small stellate and pyramidal types. The nuclei are small round and oval in shapes containing single or multiple particles.

(c) The central area consists chiefly of small stellate cells. A few pyramidal, fusiform, and large stellate cells are also present. The cells and nuclei merge with those of the stratum griseum periventriculare and the stratum album centrale of the optic tectum.

(B) Fibro-architecture.

(a) The non-myelinated fibres predominate markedly over the myelinated fibres.

(b) The central area consists of a network of fibres which is continuous with its fellow of the opposite side and is connected with the optic tectum of the same side by the fibres of the stratum album centrale and the peri-ventricular network of the latter. A bi-lateral correlation is thus established between the/

the optic tectum and the torus semicircularis. It is further connected with the nucleus isthmi and tractus octavomesencephalicus of the same side.

Class - Aves.

Sub-class - Neornithes.

Order - Neognathae (Carinatae).

Sub-order - Galliformes.

Species - Gallus domesticus
(domestic fowl).
Age - 1 Day - 30 Days,
and 2 yrs. (+).

MEASUREMENTS.

I. (a) Weight of the body - 1814.0 gm.

(b) " " " brain - 4.0 gm.

II. (a) Length of the brain - 3.2 cm.

III. Optic lobe:

(a) Antero-posterior - 1.0 cm.

(b) Transverse - 0.6 cm.

IV. Cerebrum:

(a) Antero-posterior - 2.0 cm.

(b) Transverse - 1.2 cm.

V. Cerebellum:

(a) Antero-posterior - 1.2 cm.

(b) Transverse - 0.6 cm.

MACROSCOPIC OBSERVATIONS.

I. Adult Structure.

Each optic lobe is ovoid in shape with its long axis directed downward, forward, and outward. Its upper pole is more pointed, having a smaller radius of curvature than the lower and is situated more medially. Each lobe is placed on the side of the brain stem and lies between the cerebrum anteriorly and cerebellum posteriorly. Each is/

is white in colour being covered on the surface by a thick sheet of nerve fibres belonging to the marginal optic tract. The optic lobe has three surfaces - medial, anterior, and posterolateral. The medial surface is fused with the brain stem i.e. with the diencephalon rostrally and mesencephalon caudally. The anterior surface is flat and oval in shape. It lies in contact with the overlapping cerebral hemisphere. The postero-lateral surface is convex in all directions and is separated from the cranial cavity by the meninges of the brain. The antero-medial and postero-medial borders, which bound the medial surface, are continuous above and below, and correspond in position to the sulcus limitans optici (Sutler, E., 1943), which demarcates the lobe from the surrounding parts. The convex lateral border separates the anterior from the postero-lateral surface.

The large size of the optic lobe relative to the size of the brain as a whole, is well shown in the photographs (Fig. 24) and has been accounted for by the large size of their eyes and also by their visual reflex activities (Huber & Crosby).

Like the other submammalian forms the optic lobe in birds also contains a cavity, called the <u>optic ventricle</u>.

As/

As may be seen with the naked eye in a transverse section of the optic lobe, this cavity is slit like and is the lateral extension of the aqueduct of the midbrain. The cavity thus communicates with the aqueduct as also with its fellow of the opposite side. As in the rest of the submammals it divides the optic lobe into a roof, the optic tectum, and a convex floor, which merges with the tegmentum. The roof and the floor meet at the lateral recess of the slit, which, however, as stated already, does not represent the sulcus limitans of the aqueduct. The floor contains the nucleus mesencephalicus lateralis pars dorsalis, a structure homologous with the torus semicircularis of the still lower forms. The optic ventricle, as in the frog and lizard, does not extend to the caudal limit of the optic tectum. The nucleus mesencephalicus lateralis pars dorsalis throughout its extent occupies a lateral position lying in the floor of the optic ventricle, and unlike the frog and lizard, does not approach the median plane to undergo fusion with its fellow of the opposite side. This is probably due to the lateral position of the optic lobe which has been pushed to the side by the remarkable growth of the cerebrum and the cerebellum as well.

II. Development./

II. Development.

Table 4 shows the relationship between the weight of the brain at different ages and the corresponding body weight. It is clear from the table that the weight of the brain of Gallus domesticus in relation to the body weight diminishes markedly during the period of development subsequent to hatching.

Table 5 shows the lengths at different ages of the optic lobe, cerebellum, and cerebrum expressed as percentages of the total length of the brain. For economic reasons it was not practicable to determine the weight of the optic lobe directly as this would have entailed the destruction of many valuable specimens. As may be seen by superimposing a tracing of a photograph of the lateral aspect of an adult brain (2 yrs. 2 months) suitably reduced in size of a corresponding tracing of a one-day old brain there is no remarkable change in the shape of the three parts of the brain under discussion. For this reason it is considered that the growth changes of the three parts of the brain and the optic lobe in particular can be estimated by the measurement of the greatest length of these parts as shown in the figure (Fig. 25). The table shows that the ratio of length of the optic lobe to the

whole/

Table 4. Table showing the relation between the weight of the brain at different ages and the corresponding body weight.

Age	Weight of brains in gms.	Weight of body in gms.	Ratio
1 day	1.05	39.0	1:37
2 days	1.05	39.0	1:37
3 "	1.01	44.0	1:43.5
4 "	1.11	48.0	1:43.3
5 "	1.11	51.0	1:46
6 "	1.15	53.0	1:46
7 "	1.27	55.0	1:43
8 "	1.26	69.0	1:54.8
9 "	1.28	52.0	1:40.6
10 "	1.39	77.0	1:55.3
12 "	1.51	86.0	1:56.9
16 "	1.65	124.0	1:75.2
18 "	1.85	155.0	1:83.8
20 "	1.80	123.0	1:68.3
25 "	2.13	265.0	1:124.4
30 "	2.40	320.0	1:133.3
2 yrs. 2 mths.	4.0	1814.0	1:453.5

Table 5. Table showing the lengths at different ages of the optic lobe, cerebellum, and cerebrum expressed as percentages of the total length of the brain.

Age	Optic lobe	Cerebellum	Cerebrum
1 day	38.8 %	44.4 %	61.1 %
2 days	38.8 %	44.4 %	61.1 %
3 "	38.8 %	44.4 %	61.1 %
4 "	36.8 %	42.1 %	57.9 %
5 "	36.8 %	42.1 %	57.9 %
6 "	36.8 %	42.1 %	57.9 %
7 "	35.0 %	40.0 %	60.0 %
8 "	35.0 %	40.0 %	60.0 %
9 "	35.0 %	40.0 %	65.0 %
10 "	36.8 %	47.4 %	65.8 %
12 "	38.1 %	42.9 %	66.6 %
16 "	36.4 %	40.9 %	59.0 %
18 "	36.4 %	40.9 %	63.7 %
20 "	34.8 %	39.0 %	60.7 %
25 "	37.5 %	39.5 %	62.5 %
30 "	31.2 %	37.5 %	65.5 %
2 yrs. 2 mths.	34.5 %	41.3 %	58.6 %
Mean Value	36.3 %	41.7 %	62.2 %

whole length of the brain diminishes with growth during the period after hatching. There is a similar diminution in the ratio of the length of the cerebellum, but no such diminution could be found in respect of the cerebrum (Fig. 26).

It is thus apparent that during the period of development after hatching the optic lobe diminishes in length in respect to that of the brain and body as a whole. At all ages the optic lobe is smaller than the cerebrum or the cerebellum. Photographs of the brains of a chicken, aged 1 day, and an adult hen, aged 2 yrs. 2 months, will also verify these findings (Figs. 24, 26).

MICROSCOPIC OBSERVATIONS.

A. OPTIC TECTUM.

I. Adult Structure.

The layers of the optic tectum have been studied by different workers in the past. So far the literature is available this study dates back to 1888 when Bellonci described 7 layers. The subsequent workers have given the number of layers in the optic tectum as follows:-

1. van Gehuchten ('92) - 3 layers.

2./

2. von Kölliker ('96) - 9 layers.

3. Ris ('99) - 9 layers.

4. Ramón y Cajal ('09 & '11) - 16 layers.

5. Scharrer & Sinden ('49) - 17 layers.

6. Takuji Shirasu ('52) - 15 layers.

7. Cragg, Evans, & Hamlyn ('54) - 7 layers.

The author has restricted his studies chiefly to the normal histology of the optic tectum in Gallus domesticus at different ages and has found 16 layers which have been named from without inwards (Fig. 27). In table 6 the author has tried to correlate the layers, as defined by him, with those of some of the previous workers.

This differentiation into so many layers would be more interesting could it be correlated with functions, which are still very obscure, nothing much being known as yet.

The stratum opticum consists of lateral fibres of the optic tract, called the marginal optic tract. The fibres reach the rostral end of the optic lobe ventro-medially and spread out dorso-caudally to form the most superficial layer of the lobe. The density of the fibres is greatest where they enter the lobe, but gradually becomes thinner as they sweep backward and out-

ward/

Table 6. Comparison of the author's classification of the layers of the optic tectum with that of other workers.

Number of layers	Author's Observations	Cragg, Evans & Hamlyn (1954)	S. Ramón Cajal (1911)
1	Stratum opticum (St.o.)	(1) Optic fibre layer (O.f.l.)	Layer 1.
2	Fibre layer	(2) Superficial Plexiform layer (S.pl.l.)	Layers 2 & 3.
3	Cell layer		Layer 4.
4	Fibre layer		Layer 5.
5	Cell layer		Layer 6.
6	Fibre layer		Layer 7.
7	Cell layer		Layer 8.
8	Fibre layer		Layer 9.
9	Cell layer		Layer 10.
10	Fibre layer		Layers 11 & 12.

Stratum fibrosum et griseum superficiale (St. f. et g.sup.)

(3) Radial fibre layer (R.f.l.)

11/

Table 6. (Cont'd.)

Number of layers	Author's Observations	Cragg, Evans, & Hamlyn (1954)	S. Ramón Cajal (1911)
11	Stratum griseum centrale (St.g.c.)	(4) Deep plexiform layer (D.pl.l.)	Layer 13.
12	Stratum album centrale pars superficialis (St.a.c.s.)	(5) Central fibre layer (C.f.l.)	Layer 14.
13	Stratum album centrale pars profundum (St.a.c.p.)		
14	Stratum griseum peri-ventriculare (St.g.p.)	(6) Perivent-ricular layer (P.v.l.)	Layer 15.
15	Stratum fibrosum peri-ventriculare (St.f.p.)		
16	Stratum ependymale (St.e.)	(7) Ependymal layer (E.l.)	Layer 16.

ward disappearing ultimately on the dorsal aspect of the lobe. This layer corresponds with layer 1 of S. Ramón Cajal ('11), and optic fibre layer of Cragg, Evans, and Hamlyn ('54).

The stratum fibrosum et griseum superficiale consists of alternate fibre and cell layers comprising of layers 2 to 10. It corresponds with layers 2 to 12 of S. Ramón Cajal ('11) and forms the major receptive field for the optic fibres.

Layer 2 has been named "the superficial plexiform layer" by Cragg, Evans, and Hamlyn ('54) probably because of the plexiform arrangement of its fibres. It lies just beneath the stratum opticum (layer 1), the fibres of which, bending inward, enter this layer on their way to the deeper layers, with the cells of which they come into synaptic relations constituting the chief afferent fibres of the optic tectum. The layer receives also the radial fibres from the subjacent layers.

The "radial fibre layer" of Cragg, Evans, and Hamlyn ('54) constitutes layers 3 to 10. This was so called probably because the radial fibres form the most characteristic feature of the layers in both iron-haematoxylin and silver preparations. The radial fibres have/

have been described as the apical dendrites of the pyramidal cells of the optic tectum.

The stratum griseum centrale (layer 11) should better be called "the stellate cell layer" as large stellate cells predominate. The cells are regarded to form the efferent neurons of the optic tectum. The layer is homologous with layer 13 of Ramón and Ramón y Cajal ('11). Cragg, Evans, and Hamlyn ('54), however, called this layer "deep plexiform layer" probably because of the plexiform arrangement of its fibres. The axons of these cells passing through the subjacent layers constitute the great efferent pathways of the optic tectum.

Depending on the density of staining in iron-haematoxylin preparations, the stratum album centrale has further been differentiated into two distinct zones viz., (i) a superficial relatively denser zone, called the stratum album centrale pars superficialis (layer 12), and (ii) a deeper lighter zone, the stratum album centrale pars profundum (layer 13). Both these layers constitute pathways for the efferent impulses of the optic tectum (Kappers, Huber, and Crosby, '36; Cragg, Evans, and Hamlyn, '54). It corresponds with layer 14 of Cajal ('11) and "central fibre layer" of Cragg, Evans, and Hamlyn/

Hamlyn ('54).

The periventricular layers in the bird - stratum griseum periventriculare (layer 14) and stratum fibrosum periventriculare (layer 15) - are markedly reduced, most of their gray having migrated peripherally (Kappers, Huber, and Crosby, '36). They are homologous with layer 15 of Cajal ('11) and "the periventricular layer" of Cragg, Evans, and Hamlyn ('54).

The stratum ependymale is the innermost layer of the optic tectum and lines the optic ventricle. It corresponds with layer 16 of S. Ramón Cajal ('11), and "the ependymal layer" of Cragg, Evans, and Hamlyn ('54).

Carbol-fuchsin preparations (Figs. 27, 28).

Layer 1 (stratum opticum):

This is a fairly broad zone and presents innumerable small round and oval nuclei without any apparent cytoplasm and containing distinct particles. The nuclei are mostly arranged in parallel rows. Some of the nuclei are a little larger than the others. A few pyramidal, fusiform, and small stellate cells are also scattered here and there. Dorsally and ventrally the layer is limited by the sulcus limitans optici (Fig. 28). Many blood vessels/

vessels are seen to enter this layer from the surface.

Layers 2 to 10 (stratum fibrosum et griseum superficiale):

All these layers taken together constitute about half the thickness of the optic tectum. The cell density of this stratum is very high. The cells and nuclei are more crowded in layers 3, 5, 7, and 9, but are loosely scattered in others. Layer 5 is the thinnest of all the layers having a cell density of about one to two rows only, as seen in the transverse sections. Layer 7 is a little thicker than the preceding one consisting of a few rows of cells and nuclei. Layer 3 is intermediate in thickness between layer 7 and layer 9, which is the thickest of all.

The cells predominantly belong to the following types in order of their frequency of occurrence:-

(a) Stellate cells: these are of the smaller variety being about half the size of those present in the stratum griseum centrale and measuring about 20µ in diameter. They should better be called the small stellate cells. These cells constitute the largest number amongst the other types and lie scattered through all the layers.

(b) Fusiform cells: these are also present in fairly large number and are distributed in all the layers.

(c)/

(c) Pyramidal cells: these are mostly of the large pyramidal type being mixed up with a few small pyramidal cells. These cells, however, form the characteristic feature of layer 9.

Besides these cells, a large number of round and oval nuclei, as described in relation to the previous layer, are also scattered all throughout the layers.

Dorsally the layers are limited by the sulcus limitans optici and ventrally by a relatively clearer zone, which, in iron-haematoxylin preparations, is occupied by the tecto-bulbar fibres. (Fig.30).

Layer 11 (stratum griseum centrale):

This is a broad cellular zone becoming narrower dorsally. Plenty of large stellate cells characterise this layer. Some of the largest cells measure about 40 μ in diameter and their cytoplasm contains abundant coarse Nissl granules. The cells are diffusely scattered with distinct intercellular spaces between them. Besides, a few /

few fusiform, pyramidal, and small stellate cells, and a large number of round and oval nuclei, as in the previous layers, are scattered throughout the layer.

This layer, too, is limited both dorsally and ventrally in the same way as the previous layers.

Layers 12 and 13 (stratum album centrale pars superficiale and stratum album centrale pars profundum):

Each of these layers is almost as broad as the previous one and appears to be relatively clearer consisting mostly of nuclei without cytoplasm and a few cells.

The cells belong to all the types, described in relation to the previous layers; but predominantly they are of the small stellate variety. A few large stellate cells are also scattered here and there. Throughout the layers the cells and nuclei are very diffusely scattered.

The layers merge dorsally with the roof of the optic tectum and ventrally with the tegmentum.

Layer 14 (stratum griseum periventriculare):

This is a very narrow zone consisting only of 2 to 3 rows of cells distributed very irregularly in a diffuse manner. The cell density increases dorsally where they form a few rows deep. The cells are mostly of the small stellate type, though all varieties of cells, described in the/

the previous layers, are present.

Ventrally the layer merges with periventricular gray in the floor of the optic ventricle round its lateral recess. Dorsally, however, it merges with the roof of the ventricle where the latter communicates with the aqueduct, but caudal to this communication it merges with the periventricular gray in the floor of the optic ventricle.

The mesencephalic nuclei of the trigeminal nerve appear as large cells of varying shapes - round, oval, piriform, and rectangular, and contain multiple Nissl granules. They are diffusely scattered along the peripheral zone of this layer on the lateral and dorso-lateral aspect of the optic ventricle; but are more aggregated in the roof of the optic tectum adjoining the median plane where they are distributed in the form of a transverse chain.

The cells extend from the level of posterior commissure rostrally to that of trochlear nucleus caudally gradually decreasing in number.

Layer 15 (stratum fibrosum periventriculare):

Like the previous layer this is also a very narrow zone but relatively clearer in appearance. The cells are very few in number and belong mostly to the small stellate type. They are scattered very diffusely.

Ventrally/

Ventrally the layer is continuous into the floor of the optic ventricle round its lateral recess. Dorsally, however, it is continuous with its fellow of the opposite side along the tectal roof, but caudal to the communication of the optic ventricle with the aqueduct it is continuous with the floor of the ventricle.

Layer 16 (stratum ependymale):

This layer consists of about 1 to 3 rows of round and oval nuclei without any apparent cytoplasm.

Rostrally at the level of the posterior commissure there is a proliferation of these nuclei in the median plane to form the sub-commissural organ.

Iron-haematoxylin preparations (Figs. 29, 30, 31).

Layer 1:

The layer consists of closely packed myelinated fibres. Rostrally it is broader both dorsally and ventrally, but narrower laterally. Caudally, however, the dorsal width gradually diminishes till it is thinned out towards the median plane. The fibres are cut into different lengths and are disposed obliquely and at right angles to the surface in the dorsal half of the optic tectum, whereas in the ventral half they are more or less transverse. A large

number/

number of cross-sections of fibres are also present throughout the layer.

Rostrally the layer is continuous dorsally with tractus opticus marginalis pars medialis and ventrally with tractus opticus marginalis pars lateralis of the optic tract. The fibres of this layer also enter the next deeper layer (i.e. layer 2) to join the plexiform network of the latter. Caudally and ventrally the layer is further continuous with the ventral part of the stratum album centrale.

Layers 2 to 10:

Except layer 2, which presents a plexiform network of fibres, the radial fibres form the characteristic feature of the remaining layers. Probably this led Cragg, Evans, and Hamlyn ('54) to name layer 2, the outer plexiform layer, and layers 3 to 10, the radial fibre layer.

Layer 2 is a narrow zone of plexiform network of fibres. As described previously, it is continuous peripherally with the stratum opticum. Centrally, however, the faintly stained radial fibres from the deeper zones are found to enter this layer freely.

Layers 3 to 10 have been considered together, as separate differentiation of individual layers is not possible. The/

The layers consist of both radial and transverse fibres. Both sets of fibres show very distinctly in the deeper zones i.e. layers 9 and 10. The more superficial layers i.e. layers 3 to 8, however, are characterised by the presence of radial fibres which are very faintly stained in the peripheral zones. Of course, occasional small segments of transverse fibres can be seen scattered here and there. Layers 9 and 10 present also a few cross sections of fibres.

The radial fibres generally appear singly and are thicker centrally and thinner peripherally. Centrally they are continuous with similar fibres of the deeper layers, while peripherally they are found to enter layer 2, described already.

The transverse fibres of the deeper zones, on the other hand, also seem to appear singly. Dorsally they merge with tractus septo-mesencephalicus pars tectalis, while ventrally they do so with the stratum album centrale.

Besides these fibres, described already, rostrally and dorsally layers 9 and 10 present also small bundles of irregularly disposed fibres, the general inclination of which shows that they probably merge dorsally with the tractus septo-mesencephalicus pars tectalis.

Layer 11:/

Layer 11:

The fibres of this layer have the same characteristic features and distribution as those of layers 9 and 10 except that the transverse fibres, instead of being present singly, appear in small bundles. The layer as a whole presents a plexiform appearance which probably led Cragg, Evans, and Hamlyn ('54) to name it "the deep plexiform layer".

The radial fibres of this layer enter the deeper layers centrally and superficial layers peripherally. The transverse fibres, on the other hand, merge centrally with similar fibres of the next deeper layer, the stratum album centrale pars superficialis.

Layers 12 and 13:

These layers, too, like the previous one, consist of both transverse and radial fibres. The transverse fibres predominate markedly and constitute the most characteristic feature of the layers. The layers, in these preparations, stand out more prominently than the others having the thickest myelinated fibres and the greatest density of staining. Of the two layers again, the density of staining is greater in layer 12 than in 13 probably because of the greater crowding of fibres in the former. There is, however, a greater crowding/

crowding of fibres, in general, in the ventral half than in the dorsal half of the layers. A large number of cross sections of fibres are also present throughout the layers.

The transverse fibres, as in lizard, appear as small segments of compact bundles, arranged in parallel laminae, which radiate externally at right angles to the ventricular wall. Dorsally the fibres decussate in the posterior commissure rostrally and commissura tecti further caudally. Ventrally they bend medially round the lateral recess of the optic ventricle and enter the tegmentum constituting the dorsal and the ventral tecto-bulbar tracts. In the tegmentum the fibres of the dorsal tecto-bulbar tract establish relations with the different tegmental neurons of the same side including the red nucleus and ultimately decussate in the mèdian plane in the dorsal tegmental decussation. The fibres of this tract, moreover, enter the nucleus mesencephalicus lateralis pars dorsalis ventrally and medially; further they come into relation with the ventral neurons of the oculomotor nucleus. Besides, they are also connected with the medial longitudinal bundle which probably indirectly connects the optic tectum with the oculomotor as well as the trochlear nuclei . No

direct/

direct connection of these fibres can, however, be found with the trochlear nucleus. The ventral tecto-bulbar tract, likewise, also comes into relation with the ventral tegmental neurons of the same side and decussates in the median plane in the ventral tegmental decussation. By these dorsal and ventral tegmental decussations the optic tectum probably comes into relation with the different contra-lateral tegmental neurons as well. The ventral part of the layers is very intimately connected with the magnocellular and the parvocellular parts of the nucleus isthmi and, in fact, forms some sort of a capsule for the nuclear masses. Most ventrally, however, the layers merge caudally with the ventral part of the stratum opticum.

The radial fibres of the layers, on the other hand, are continuous peripherally with the superficial layers and centrally with the periventricular network.

Besides the fibres, described already, layer 12 presents also small segments of irregularly scattered bundles, especially rostrally and dorsally. It appears from their mode of distribution that probably they merge dorsally with the tractus septo-mesencephalicus pars tectalis. /

tectalis.

Layers 14 and 15:

These layers consist of a network of fine fibres the density of which is a little greater in layer 15 than in the other. Peripherally the network is continuous with the radial fibres. Ventrally it merges with a similar network in the floor of the ventricle round its lateral recess. Dorsally and rostrally it is continued in the posterior commissure. Further caudally it does so in the decussatio tecti. Still further caudally it is continuous again with a similar network of the floor of the ventricle.

The mesencephalic roots of the trigeminal nerve appear as small bundles of fibres of varying lengths in the peripheral zone of layer 14 as well as in the roof of the ventricle and aqueduct. They extend from the caudal level of the posterior commissure to the level of the trochlear nucleus.

Layer 16:

This layer does not contain any fibresin these preparations.

Silver preparations.

These corroborate the observations of the iron-haematoxylin/

haematoxylin preparations with the following alterations:

(i) The radial fibres of layers 3 to 10 and plexiform network of layers 2, 14, and 15 are more distinct and numerous in these preparations. Thus it is clear that in these layers there is a marked predominance of the non-myelinated over the myelinated fibres.

(ii) The continuity of the radial fibres of layers 3 to 10 with the network of layer 2 is further quite evident.

II. Development.

The following table shows the thickness in μ of different layers of the optic tectum in Gallus domesticus at different ages at the level of the oculomotor nucleus as evident from the projection drawings:

Age/

Age	Stratum opticum (=L.1)	Stratum fibrosum et griseum superficiale. (=L.2 to 10)	Stratum griseum centrale (=L.11)	Stratum album centrale (=L.12 & 13)	Stratum griseum et fibrosum periventriculare. (=L.14 & 15)	Stratum ependymale (=L.16)
1 day	17-34µ	444-462µ	150-158µ	192-205µ	51-85µ	13-26µ
2 yrs.(+)	111-145µ	555-607µ	158-196µ	205-239µ	59-118µ	17-26µ

It is evident from the table that as age advances the growth is more marked in the receptive than in the discharge zones of the optic tectum. It is greatest in the stratum opticum, less in the stratum fibrosum et griseum superficiale, and still less in the other layers (Fig. 32). In this process of growth, however, the size of the cells and nuclei does not change. For example the large stellate cells of the stratum griseum centrale retain a diameter of about 40μ at all ages. This increase is, therefore, in the intercellular substance which has been termed "the integration organ" by Bauer.

Carbol-fuchsin preparations.

No appreciable change is noticed in any layer between 1 day old and adult age except that there is some increase of the intercellular spaces as growth progresses (Figs. 35, 27). This is more clearly evident in the stratum griseum centrale (layer 11) where the cells are more closely crowded in 1 day old chick, but are separated by well spaced intervals in the adult age. As already stated, the size of the cells and nuclei, however, does not change as age advances. This is also proved by the fact that in both 1 day old and adult age the large stellate cells/

cells of the stratum griseum centrale measure about 40 μ in diameter (Figs. 33, 34).

Iron-haematoxylin preparations (Figs. 29, 36)

Myelination of fibres, as indicated by the staining of the neurokeratin derived from the myelin sheaths, gradually increases as age advances. This is evident from table 7 where the depth of staining of the fibres of different layers of the optic tectum in respect to the age has been indicated. It is considered that, although all the myelinated fibres may not have been stained, the myelin sheaths were rendered visible at a certain stage of their development, and that the order of this development is thereby shown in the table.

Layer 1:

A very marked change is observed in this layer during the period of growth after hatching. The staining of myelin is very faint during the first few days. From the 7th day onward it increases in depth. It is first evident where the fibres of the optic tract enter the optic lobe and subsequently spreads throughout the layer. The layer is much thicker in adult age than in the 1 day old chick.

Layers 2 to 10: /

Table 7. Table indicating the depth of staining of myelin sheaths in iron-haematoxylin preparations for the different layers of the optic tectum in Gallus domesticus at different ages.

Age	Stratum opticum (=L.1)	Stratum fibrosum et griseum superficiale		Stratum griseum centrale (=L.11)	Stratum album centrale (=L.12 & 13)	Stratum griseum et fibrosum periventriculare (=L.14 & 15)
		(L.2)	(L.3 to 10)			
1 day	+	-	+	+	++	-
2 days	+	-	+	+	++	-
7 "	++	-	+	++	+++	-
9 "	++	-	++	+++	++++	-
12 "	++	-	++	+++	++++	-
16 "	++	-	++	+++	++++	-
18 "	+++	-	++	+++	++++	-
20 "	+++	+	++	+++	++++	-
25 "	+++	+	+++	+++	++++	-
30 "	+++	++	+++	+++	++++	+
2 yrs.(+) (adult)	++++	+++	++++	++++	+++++	++

Layers 2 to 10:

Layer 2 does not show any staining of the fibres in the first or subsequent few days after hatching. On the 20th day after hatching the staining is very faint, but becomes distinct in the adult form.

The fibres of layers 3 to 10, especially of layer 9 and 10, stain very faintly in the first few days after hatching. The depth of staining increases as age advances. The fibres become distinctly stained from the 7th to 9th day onward after hatching. They show very clearly in the adult age.

Layer 11:

In the first few days after hatching the fibres stain very faintly. The density of staining increases as age advances. From the 7th day onward after hatching the fibres show very clearly till the adult age is reached when they appear most distinct.

Layers 12 and 13:

The fibres of these layers, in contrast to all the other layers of the optic tectum, stain very distinctly even from the first day after hatching (Fig.36). These layers /

layers show thus the earliest myelination. The intensity of staining increases as age advances and becomes the greatest in the adult age.

Layers 14 and 15:

The fibres in these layers do not show up to 18th day after hatching. On the 20th day they stain very faintly. The density of staining increases gradually with age, and in the adult age becomes most distinct. At all ages, however, the density of staining is less than that of the stratum album centrale.

The fibres of the posterior commissure, commissura tecti, tractus septo-mesencephalicus tecti and mesencephalic roots of the trigeminal nerve show distinct myelination from the very first day after hatching. The depth of staining of these fibres, however, increases with age.

Silver preparations

The /

The fibres in all the layers at all ages impregnate very distinctly with silver. For a few days after hatching the proportion of non-myelinated fibres and of fibres too thinly myelinated to stain with iron haematoxylin is much greater than that of the definitely myelinated fibres, which gradually replace the former as age advances. Further, there is a distinct increase of fibres in the stratum opticum as development progresses after hatching.

B. NUCLEUS MESENCEPHALICUS LATERALIS PARS DORSALIS

I. Adult Structure

It lies in the floor of the optic ventricle (Fig.28) throughout its rostro-caudal extent and has been so called by Ariens Kappers ('21). Wallenberg ('98), however, named it "ganglion laterale". The author cannot understand why it has been called by the previous workers "the homologue of the torus semicircularis" of the other submammalian forms, though it has the same position and connexions.

It appears at the caudal part of the posterior commissure /

ure immediately rostral to the oculomotor nucleus, and extends caudally up to the level of the trochlear nucleus. At the level where it is well formed it presents an oval shape in transverse section with the long axis directed ventrally and laterally (Figs. 28, 30). Unlike the frog and lizard, it occupies a more lateral position and does not approach the median plane to undergo fusion with its fellow of the opposite side. Through its entire rostro-caudal extent it lies under cover of the optic tectum.

Carbol fuchsin preparations (Fig. 37).

The cells and nuclei are scattered very diffusely. The cells consist chiefly of the stellate type - small and large. The large stellate cells are more numerous in the central zone of the nuclear mass and separated from one another by well spaced intervals as in the stratum griseum centrale of the optic tectum. A few fusiform and pyramidal cells are also scattered here and there. Besides these cells, a large number of small round and oval nuclei without any apparent cytoplasm, as seen in the optic tectum, are also present throughout the nuclear mass.

Dorsally/

Dorsally and laterally it merges with the stratum griseum periventriculare of the floor of the optic ventricle and is separated from the ependymal lining of the ventricle by the relatively clear zone of stratum fibrosum periventriculare. Dorso-medially it merges with the cells of the tegmentum. Ventro-laterally it is continuous with the stratum griseum periventriculare of the optic tectum. Ventro-medially and ventrally it is separated from the tegmental neurons by a relatively clear zone, which, in the iron-haematoxylin preparations, is occupied by the tecto-bulbar fibres (Fig. 30).

More caudally, however, it is continuous with the stratum griseum periventriculare of the optic tectum both dorsally and ventro-laterally round the margins of the optic ventricle.

Iron-haematoxylin preparations (Figs. 30, 31).

It consists of a network of myelinated fibres the density of which is greater medially and ventrally. Laterally the network is continuous with that of the periventricular layers of the floor of the optic ventricle as well as of the optic tectum.

Dorso-medially and rostrally it is continuous with the/

the periventricular layers of the tegmentum; further caudally, however, it is not only continuous with that of the tegmentum, but also with its fellow of the opposite side through the decussatio tecti. Fibres of the tecto-bulbar tract are seen to enter this zone ventrally. Ventrally and ventro-medially it is further connected by radial fibres with those the tegmentum; further caudally it is connected with the fibres of the lateral lemniscus.

Caudally the fibre bundles from its ventro-medial aspect are continued into the ventral tecto-bulbar tract.

Silver preparations.

These corroborate the findings of the iron-haematoxylin preparations with the difference that the plexiform network of fibres and the fibre bundles show more distinctly.

II. Development.

Carbol-fuchsin preparations.

The cells are more closely crowded in 1 day old (Fig. 38) than in adult age where they are more diffuse with definite increase of the intercellular spaces (Fig. 37).

The/

The size of the cells, however, does not increase with increasing age, but remains the same at all ages. This is also evident from the fact that some of the large stellate cells measure about 40µ in diameter at all ages. Thus, as age advances, there is an increase of the intercellular material which Bauer termed "the integration organ".

Iron-haematoxylin preparations.

From table 8 it is evident that myelination of fibres increases as age advances and reaches its maximum in the adult age. In the first few days after hatching the fibres are stained very faintly. The staining of fibres is distinct on the 7th day and gradually increases with increasing age.

Silver preparations.

At all ages the fibres show very distinctly and to a greater extent than in the iron-haematoxylin preparations. There is also a general increase of fibres as age progresses. It is thus evident that the amount of non-myelinated fibres is much greater in the earlier ages. They become more and more myelinated as age increases.

Table 8. Table illustrating the depth of staining in these preparations to show the extent of myelinations of its fibres at different ages after hatching.

Age	1 to 6 days	7 days	9 days	12 days	16 days	18 days	20 days	25 days	30 days	2 yrs. (+) (Adult)
Nucleus mesencephalicus lateralis pars dorsalis	+	++	++	++	++	+++	+++	+++	++++	+++++

REVIEW OF THE OBSERVATIONS

A. Macroscopic Observations

I. Adult Structure.

(a) The optic lobes in birds (Gallus domesticus) are very well developed. This is clearly evident in the photographs.

(b) Of the three main parts of the brain, the optic lobe is the smallest, the cerebrum the largest, and the cerebellum intermediate in size between the two.

(c) Unlike the rest of the submammals each lobe is placed on the side of the brain-stem being partially overlapped by the cerebrum and the cerebellum, which overlap each other to a certain extent in the median plane dorsally.

(d) Each lobe is white in colour being covered by the fibres of the marginal optic tract and is encircled by the sulcus limitans optici which demarcates it from the surrounding parts.

(e) /

(e) Each lobe, like other submammals, contains a cavity, the optic ventricle, which demarcates the lobe into a roof, the optic tectum, and a convex floor, which merges with the tegmentum.

The optic tectum is concerned with vision and is homologous with the mammalian superior colliculus. The floor contains the nucleus mesencephalicus lateralis pars dorsalis, a structure which is homologous with the torus semicircularis of the other submammals and inferior colliculus in mammals, and is auditory in function.

(f) The optic ventricle is slit like and is the lateral extension of the aqueduct. Its lateral recess does not indicate the position of the sulcus limitans.

(g) As in the frog and the lizard the optic ventricle does not extend to the caudal limit of the optic tectum.

(h) The nucleus mesencephalicus lateralis pars dorsalis, contained in the floor of the ventricle, does not approach the median plane to undergo fusion with its fellow of the opposite side as it does in the frog and lizard.

II. Development.

(a) Weight of the brain diminishes remarkably in relation to/

to the weight of the body during the period of development after hatching.

(b) The optic lobe diminishes in length in respect to that of the brain and body as a whole as age advances subsequent to hatching.

B. Microscopic Observations - Optic tectum

I. Adult Structure.

(a) The optic tectum in this form consists of 16 layers which have been named from without inward in accordance with Huber and Crosby's observations on the reptilian tecti ('33).

(b) This lamination of the optic tectum is very distinct and has attained the maximum development in this form.

(c) The periventricular layers are markedly reduced and the receptive zone (i.e. layers 1 to 10) constitutes the greatest thickness of the optic tectum.

(d) Cyto-architecture.

(i) The cells of the optic tectum consist of the stellate, fusiform, and pyramidal types.

(ii) The small stellate cells, measuring about 20μ in diameter, constitute by far the largest number and are present in almost all the layers,

(iii) The large stellate cells, about 40μ in diameter approximately,/

approximately, form the characteristic feature of the stratum griseum centrale (layer 11).

(iv) The pyramidal cells are found particularly in layers 3 and 7.

(v) The fusiform cells are present in almost all the layers.

(vi) Unlike the other submammals, fish, frog, and lizard, the periventricular layers, in bird, are markedly reduced and contain very few cells.

(vii) The mesencephalic neurons of the trigeminal nerve appear as large isolated cells of varying shapes - round, oval, piriform and rectangular, and contain multiple Nissl granules.

They are distributed in the form of a chain in the roof of the ventricle and the aqueduct, but are diffusely scattered in the peripheral zone /

zone of the stratum griseum periventriculare (layer 14), especially in its dorsal part.

They extend from the level of the posterior commissure rostrally to that of the trochlear nucleus caudally.

Their number gradually declines caudally.

(viii) The subcommissural organ appears as an aggregation of the ependymal cells in the roof of the ventricle just deep to the posterior commissure.

(e) Fibro-architecture.

(i) The fibres of the marginal optic tract reaching the optic lobe ventrally and rostrally at the sulcus limitans optici divide into the medial and lateral marginal tracts which sweep along the surface of the optic lobe in a rostro-caudal direction. On their way they bend inward to enter the subjacent layers.

The lateral marginal tract extends throughout the rostro-caudal extent of the optic tectum. The medial marginal tract, on the contrary, gradually thins out caudally.

The fibres of the lateral marginal tract probably/

probably enter further layers 9, 10, and 11 from their ventral aspect.

(ii) The radial fibres traverse the different layers of the optic tectum.

(iii) The transverse fibres of layers 12 and 13 (stratum album centrale pars superficialis and stratum album centrale pars profundum) decussate dorsally in the posterior commissure and the commissura tecti.

Ventrally they constitute the dorsal and ventral tecto-bulbar tracts. By these tracts they come into relation with the different tegmental neurons of the opposite side after decussating in the dorsal and ventral tegmental decussations respectively. Besides, they come into direct relation with the nucleus mesencephalicus lateralis pars dorsalis and ventral part of the oculomotor nucleus of the same side.

Further /

Further they are connected with the medial longitudinal fasciculus through which probably they are indirectly related with the oculomotor and trochlear nuclei.

Through these fibres the optic tectum is also very intimately connected with the homolateral nucleus isthmi.

(iv) The fine plexiform network of the periventricular layers is connected by commissura tecti with its fellow of the opposite side and is also continuous with a similar network of the floor of the ventricle.

II. Development.

(a) Cyto-architecture.

(i) All the layers of the optic tectum participate to a certain extent in the process of growth and development as age advances; but the superficial zone (layers 1 to 10) grows more markedly than the deeper zone, which shows little growth.

(ii) In this process of development the size of the cells, however, does not increase. It is especially evident that the size of the large /

large stellate cells in the stratum griseum centrale (layer 11) remains unchanged as development progresses with advancing age and is about 40 u in the one day old chick and at adult age.

(iii) The cells are more crowded in the one day old chick than in the adult, and the increase in growth of the optic tectum is due to an increase in the intercellular material, which, in mammals, has been termed by Bauer ('53) "the integration organ".

(b) Fibro-architecture.

As shown by Table 7 myelination has begun in all the layers of the optic tectum except perhaps in layers 2, 14 and 15 even on the first day after hatching. The depth of staining of the sheaths in iron haematoxylin preparations gradually increases as age advances, and is always greatest in the stratum album centrale.

An examination of the silver preparations indicates that there is an increase in the total number of the fibres of the opticum tectum as age advances, and that this increase is most marked in the stratum opticum. Quantitative estimations have, however, not been made.

C. Microscopic Observations /

C. Microscopic Observations - Nucleus mesencephalicus lateralis pars dorsalis.

I. Adult Structure.

(a) It occupies the floor of the optic ventricle throughout its rostro-caudal extent and lies under cover of the optic tectum.

(b) /

(b) It extends from the caudal region of the posterior commissure rostrally to the trochlear nucleus caudally.

(c) Unlike the frog and the lizard, it occupies a more lateral position and does not approach the middle line to undergo fusion with its fellow of the opposite side.

(d) It has been said to be homologous with the submammalian torus semicircularis; but structurally it resembles more the mammalian inferior colliculus and consists of an oval nuclear mass and a peripheral capsular zone.

(e) Cyto-architecture.

(i) The nuclear mass consists chiefly of stellate cells, small and large. The large stellate cells predominate in the central area of the nuclear mass and are like those of the stratum griseum centrale of the optic tectum.

Besides, a few pyramidal and fusiform cells are also present.

The nuclear mass is continuous dorsally and ventrally with the stratum griseum periventriculare of the optic tectum. Dorsally it is/

is continuous with the periventricular grey of the tegmentum.

(f) Fibro-architecture.

(i) The central nuclear mass consists of a plexiform network of fibres the density of which is a little greater ventrally and medially.

The peripheral capsular zone is occupied by the fibres of the different fibre tracts which are related to this nuclear mass.

(ii) The network is continuous with that of the periventricular layers of the floor of the ventricle and is connected with the optic tectum through the dorsal tecto-bulbar tract and the periventricular network of the latter.

It is continuous also with a similar network of the tegmentum and decussates in the commissura tecti. Besides, it is intimately connected with the nucleus isthmi and the lateral lemniscus.

II. Development /

II. Development

(a) Cyto-architecture.

(i) The cells are more crowded in the 1 day old chick than in the adult age where they are more diffuse with increase of the intercellular spaces.

(ii) The size of the cells does not change in the process of development as age progresses. For example the large stellate cells measure about 40 μ in diameter in both the 1 day old and in adult age.

(iii) There is an increase of the intercellular material as growth proceeds and this is "the integration organ" of Bauer.

(b) Fibro-architecture /

(b) Fibro-architecture.

(i) In the first few days after hatching the fibres present very little myelination. The fibres appear to show clearly from the 7th day onward after hatching.
It is evident from the table 7 that the density of the myelination increases as age advances and becomes maximum in the adult age.

Class	-	Mammalia.
Sub-class	-	Eutheria.
Order	-	Rodentia.
Sub-order	-	Simplicidentata.
Section	-	Myomorpha.
Species	-	Mus norvegicus albinus (albino rat). Age - Adult.

MEASUREMENTS.

I. (i) Length of rat - 39.0 cm.

(ii) " " brain - 3.0 cm.

II. (i) Weight of rat - 255.0 gm.

(ii) " " brain - 2.02 gm.

III. Superior colliculus:

(i) Antero-posterior - 3.0 mm.

(ii) Transverse - 3.0 mm.

IV. Inferior colliculus:

(i) Antero-posterior - 2.0 mm.

(ii) Transverse - 3.0 mm.

(iii) Supero-inferior - 4.0 mm.

V. Cerebrum:

(i) Antero-posterior - 15.0 mm.

(ii) Transverse - 7.0 mm.

(iii) Supero-inferior - 12.0 mm.

VI. Cerebellum:

(i) Antero-posterior - 8.0 mm.

(ii) Transverse - 13.0 mm.

MACROSCOPIC OBSERVATIONS.

THE TECTUM.

The/

The tectum is that part of the midbrain which lies dorsal to a transverse plane passing through the sulcus limitans of the aqueduct and extends from the posterior commissure rostrally to the emergence of trochlear nerve caudally.

It consists of a superior and an inferior pair of rounded elevations separated from one another by a cruciate sulcus. Each pair is very symmetrically developed. The anterior elevations are called the anterior, or superior colliculi, while the posterior are known as the posterior, or inferior colliculi (Fig. 39). According to the B.R. terminology they are known in the human brain as the superior and inferior corpora quadrigemina.

The longitudinal part of the cruciate sulcus flattens out posteriorly to lodge the pineal body; the transverse part, on the other hand, is directed on each side forwards and outwards and is limited laterally by an oblique groove lying between the colliculi and the thalamus. The colliculi lie below and behind the splenium of the corpus collosum and are overlapped rostrally by the cerebrum and caudally by the cerebellum. In the gap between the posterior part of the cerebrum and the anterior part of the/

the cerebellum the dorsal parts of the inferior colliculi and the pineal body can be seen from the surface (Fig. 40). The colliculi are fused with one another, the surface grooves demarcating them only superficially.

Unlike the lower vertebrates the tectum in mammals does not contain any ventricle.

A. SUPERIOR COLLICULI.

As seen from the dorsal aspect the superior colliculi are in shape equilateral triangles (Fig. 39), so that each superior colliculus can be described as having three borders, antero-lateral, medial and posterior, each measuring about 3 mm. In front of its antero-lateral border lie the habenula and the thalamus from within outward, an oblique groove intervening between them. The medial border is adjacent to its fellow of the opposite side, the longitudinal sulcus intervening between them. The posterior border is separated from the inferior colliculus by the transverse sulcus. It is thus surrounded on all sides by sulci, which demarcate it from the surrounding parts being homologous with the sulcus limitans optici of the lower vertebrates. Unlike the higher mammals/

mammals it is not overlapped by the well developed postero-lateral part of the thalamus, the pulvinar. The fibres of the optic tract sweeping round the superior surface of the posterior part of the thalamus reach the antero-lateral border of the superior colliculus carpeting the floor of the intervening groove between them. The superior brachium, unlike the higher mammals, does not form a visible surface elevation and lies in the floor of the sulcus in front of the antero-lateral border of the superior colliculus. The lateral geniculate body is also hidden from view by fibres of the optic tract. Just lateral to the lateral angle of the superior colliculus lies the medial geniculate body as an oval elevation (Fig. 39).

B. INFERIOR COLLICULI.

As seen from the dorsal surface each inferior colliculus is ovoid in shape with its long axis being directed downward, forward and outward. It produces more prominent surface bulging than the superior colliculus. Medially the two inferior colliculi are fused with each other, a shallow longitudinal sulcus intervening between them, which lodges the/

the pineal body, already described. Antero-laterally each is continuous with the inferior brachium ending in the medial geniculate body. Posteriorly it is overlapped by the cerebellum. The lateral lemniscus appears as a low ridge running upward and forward in the floor of the sulcus behind the inferior pole of the inferior colliculus (Fig. 39).

MICROSCOPIC OBSERVATIONS.

A. SUPERIOR COLLICULUS.

The structure of the mammalian tectum has been investigated by the following workers during the past 75 years (Ganser, '82; Frankl Hochwart, '02; Ramón y Cajal, '11; Winkler & Potter, '14; Castaldi, '23; Tsai, '25; and Huber & Crosby, '34). They have numbered the layers of the mammalian superior colliculus differently. The author's observations have led him to agree with the numbering of the layers as given by Kappers, Huber & Crosby ('36) which is as follows from without inward:

1. Stratum zonale.
2. Stratum griseum superficiale.
3. Stratum opticum.
4. Stratum griseum mediale.

5./

5. Stratum album mediale.

6. Stratum griseum profundum.

7. Stratum album profundum.

8. Stratum griseum periventriculare.

9. Stratum fibrosum periventriculare.

10. Stratum ependymale.

The sixth and seventh layers are homologous with the stratum griseum centrale and stratum album centrale of the submammalian optic tecta, and in the following description the latter names have been used instead of those adopted by Huber and Crosby.

According to Huber and Crosby's ('33) functional classification of the reptilian tecta the ten layers of the mammalian superior colliculus can further be reduced to 8 layers as follows (Fig. 41):

1. Stratum zonale.

2. Stratum fibrosum et griseum superficiale (=layers 2, 4, and 5.

3. Stratum opticum (=layer 3).

4. Stratum griseum centrale (= layer 6).

5. Stratum album centrale (= layer 7).

6. Stratum griseum periventriculare (= layer 8).

7. Stratum fibrosum periventriculare (= layer 9).

8./

8. Stratum ependymale (= layer 10).

Carbol-fuchsin preparations (Figs. 43, 44).

The cells of the superior colliculus are so diffusely scattered that they can only be identified with layers of the iron-haematoxylin preparations by a process of measurement carried out on projection drawings of adjacent sections.

The following description of the layers has been made possible by this method.

Layer 1:

This layer consists of a few scattered cells and nuclei, and under the low power of the microscope appears to be a relatively clear zone. One or two rows of cells lie on the surface just beneath the pia mater. The cells belong chiefly to small stellate type intermingled with a few pyramidal cells. The nuclei are small round and oval in shape containing single or multiple distinct particles. A few relatively larger nuclei may also be found here and there.

Dorso-medially this layer is continuous with its fellow of the opposite side deep to the median longitudinal sulcus. Laterally in the rostro-caudal direction it is continuous with the superficial part of lateral geniculate body,/

body, medial geniculate body, and inferior brachium, while at the caudal limit of superior colliculus it is interrupted by a triangular cluster of cells and nuclei dipping into the interior from the surface.

Layers 2-3-4:

The cells and nuclei of these layers are so diffusely arranged that it is not possible to describe them separately. They appear to form one layer which narrows dorso-medially and ventro-laterally.

The cells consist chiefly of small stellate type containing a few Nissl granules. A few large stellate cells containing multiple Nissl granules can also be seen. Besides these, there are also a large number of small round and oval nuclei scattered throughout these layers. The cells and nuclei instead of being crowded together are distributed very loosely with distinct intercellular spaces.

Dorsally these layers are continuous with those of the opposite side. Ventro-laterally the layers are limited by the dorsal part of the lateral geniculate body; further caudally they merge with the medial geniculate body and the tegmentum; still more caudally the superficial part of the layers is limited by the inferior brachium and finally/

finally stops short, while the deeper part is continuous with the tegmentum. At the caudal part of the superior colliculus the superficial part is limited by the triangular aggregation of cells, as already described, while the deeper part is directly continuous with the inferior colliculus.

Layers 5-6-7:

These layers, too, like the previous layers have been considered together as differentiation of the individual layer is not possible. Unlike the previous layers the cells and nuclei in these layers are more loosely scattered with increase of the intercellular spaces. All types of cells and nuclei, as described in the previous layers, are also present here. Besides, a great number of large stellate cells containing multiple Nissl granules are scattered throughout the layers, especially laterally. These cells constitute the most characteristic feature of these layers. Their number, however, is greatly reduced at the caudal part of the superior colliculus.

All the layers thus appear to form a single layer which narrows medially where it is continuous with its fellow of the opposite side and widens out laterally merging with the tegmentum and probably also with the deeper part of the medial geniculate body. At the caudal part/

part of the superior colliculus it merges directly with the inferior colliculus.

Layer 8:

It is a fairly broad zone of cells and nuclei which encircle the aqueduct. The cells and nuclei are like those of the previous layers, the cells being mostly of the small stellate type. The cells and nuclei, as in layers 2, 3, and 4, are loosely arranged with distinct intercellular spaces between them. The layer is a little broader laterally. Throughout its distribution, and especially dorsally, the layer is a little narrower at the level of the posterior commissure.

Dorsally the layer is continuous with its fellow of the opposite side; rostrally it merges with the group of nerve cells within the posterior commissure, which are mostly of the small stellate type.

Ventrally the layer is continued into the tegmentum where it merges with the neurons in relation to the median raphe and the oculomotor nucleus, which is characterised by the presence of large stellate cells containing multiple Nissl granules, a feature conspicuous of the motor neurons of the central nervous system.

Besides these cells and nuclei, there are also a few isolated/

isolated and large special type of cells, rounded and piriform in shape and containing multiple Nissl granules, distributed mostly in the peripheral zone of the tegmental part of this layer. These cells belong to the mesencephalic nucleus of the trigeminal nerve. The cells make their appearance at the level of the rostral part of the oculomotor nucleus and can be traced as far back as the caudal part of the inferior colliculus. At the caudal level of the superior colliculus some of these cells can be seen to extend even in the tectal part of this layer.

Layer 9:

This is a very narrow relatively clear zone containing only a few scattered cells and nuclei. The cells and nuclei are like those of the deeper part of the previous layer with which it merges very diffusely.

Layer 10:

This is the ependymal layer lining the aqueduct and consisting of from one to three rows of oval nuclei, their long axes being parallel to the ventricular surface. Rostrally at the level of the posterior commissure there is a proliferation of these ependymal cells in the roof of the aqueduct forming what is known as the sub-commissural organ./

organ.

Iron-haematoxylin preparations (Figs. 41, 42).

Layer 1:

Myelinated fibres are absent in this layer.

Layer 2:

This layer is also devoid of any myelinated fibres.

Layer 3:

The myelinated fibres of this layer are cut into short lengths and arranged into small bundles. Laterally the bundles are more obliquely placed. Medially, however, the bundles are more vertically disposed. The layer is a little broader in the central part but narrower both medially and laterally.

Laterally the layer is continuous with the optic tract, but medially it is interrupted by the median longitudinal fissure and a process of pia mater containing a blood vessel. Rostrally the layer is very prominent and distinct. The prominence gradually diminishes caudally and the fibres become more and more scanty. Very faintly stained radial fibres can, occasionally, be seen to enter this layer from the deeper zones. At the caudal limit of the superior colliculus this layer is invaded by colliculo-collicular fibres from the inferior colliculus.

Layer 4:/

Layer 4:

This layer is as broad as layer 3. The arrangement of the fibres in the lateral half of this layer is reticular in character and quite distinct from that of layer 3 except rostrally where the layers are more alike. Caudally the fibres are very indefinite.

Medially the arrangement of the fibres is indistinguishable from that of layer 3, and the boundary between the two layers has been decided arbitrarily by continuing inwards the well marked boundary line which exists between them laterally.

The fibres of layer 4 appear to be continuous laterally with those of the optic tract, and the medial and lateral geniculate body of the same side, and medially by a commissure with the fibres of the corresponding layer of the opposite side. Caudally the fibres appear to be continuous with those of the inferior colliculus of the same side.

This layer is further invaded by radial fibres from the subjacent layers.

Thus this layer has connections with subjacent layers and with the homolateral optic tract, geniculate bodies, and inferior colliculus. It is further connected/

nected with its fellow of the opposite side through the commissural fibres.

Layer 5:

This is also a broad zone of myelinated fibres. It is narrower medially gradually becoming broader in the lateral part. The fibres are cut into short lengths and arranged into small bundles. The bundles are arranged very irregularly but laterally they are obliquely disposed.

Rostrally at the level of the lateral geniculate body the transverse bundles sweep ventrally into the tegmentum along the medial aspect of the medial geniculate body. Some enter the medial geniculate body, while others continue their ventral course further and come into relation with the substantia nigra, a few bundles passing through the medial lemniscus. Some bundles are found to be continuous with similarly disposed fibre bundles of the tegmentum which coursing ventro-medially merge with the medial part of the medial lemniscus. Further caudally at the level of the medial geniculate body this layer appears to be continuous with the outer part of the medial lemniscus to enter the substantia nigra, and with the deeper part of the inferior brachium as/

as well. At the caudal part of the superior colliculus this layer, like the previous layers, is also invaded by the colliculo-collicular fibres.

Medially at the level of the posterior commissure the layer stops short at a little distance from the median plane, but the fibres of the posterior commissure can be found to enter the layer freely on each side. Moreover, at this level medially the fibres of this layer have the same mode of arrangement as those of layer 4 and seem, in fact, to be continuous with the latter as also with the medial part of layer 3. At the caudal part of the posterior commissure the layer is separated from its fellow of the opposite side by a very narrow zone of gray matter.

The radial fibres from the deeper zones enter this layer freely, so do the transverse fibres of layer 7, especially laterally.

Layer 6:

This is a relatively thinner zone and is very obscure laterally. Medially the fibres are arranged in a reticular manner. The layer is invaded by the fibres of the posterior commissure rostrally and those of the tectal commissure of the superior colliculus further caudally./

caudally. The lateral half of the layer is traversed by the transverse fibres of layer 7.

The radial fibres from the deeper zones traverse throughout the layer on their way towards the surface.

Layer 7:

This layer of the superior colliculus is most conspicuous. It is narrower medially, but becomes very broad laterally. It consists of both transverse and radial fibres.

The transverse fibres, which constitute the most prominent feature, are arranged into small bundles, cut into different lengths. Rostrally they decussate in the posterior commissure. Further caudally they do so in the tectal commissure of the superior colliculus and spread laterally into layers 5 and 6. At the caudal limit of the superior colliculus these fibres decussating in the tectal commissure spread into the inferior colliculus.

Ventrally at the level of the oculomotor nucleus the fibre bundles spread out into layers 5 and 6 on their way to the tegmentum. They then bend medially and come into relation with different tegmental neurons including substantia nigra and red nucleus. A large number of the medial/

medial bundles decussate in the median plane in the dorsal tegmental decussation. Some of these after decussation come into relation with the tegmental neurons of the opposite side as well, while others proceed further ventralward. Rostrally, however, the more medial bundles of this layer seem to enter the oculomotor nucleus of the same side. These fibres are also directly continuous with the medial longitudinal bundle. The more lateral bundles of this layer at the caudal part of the oculomotor nucleus sweep ventrally along the lateral aspect of the tegmentum and then pass medially dorsal to the cerebrospinal fibres to decussate in the ventral tegmental decussation passing through the fibres of the medial lemniscus; this feature is, however, very distinct at the most caudal part of the superior colliculus.

The radial fibres are numerous and run separately as they pass through the layer. At all levels the fibres are continuous peripherally into the more superficial layers, while centrally they enter the next deeper layer (layer 8).

Layer 8:

This layer consists of a plexiform network of very fine/

fine myelinated fibres.

At all levels dorsally the network is continuous with its fellow of the opposite side and ventrally with that of the tegmentum where it enters the network in relation with the oculomotor nucleus. Peripherally, however, it is continuous with the radial fibres of the more superficial layers.

The deeper zone of this layer rostrally consists of small bundles of fibres, cut into short lengths. The bundles are more or less vertical in the dorsal part of the aqueduct whereas in the lateral and ventro-lateral parts they are oblique.

Besides these bundles, this layer presents further innumerable cross sections of fibres especially in the lateral and ventro-lateral parts of the aqueduct. Further and further caudally the vertical bundles of fibres are replaced by more or less transverse bundles and there is further a decline in the number of fibres cut transversely.

At all levels the fibres of this deeper zone are continuous with the plexiform network of the peripheral zone.

Layer 9:

This/

This layer is a thin clear zone and in these preparations shows no fibres.

Layer 10:

It is completely devoid of any myelinated fibres.

Silver preparations.

Layer 1:

This is a relatively clear zone consisting of a plexiform network of very fine fibres, both transverse and radial. The radial fibres are continued into this layer from the deeper zones.
The layer contains further the axons of cortico-collicular fibres (Bailey, Strong, and Elwyn's Histology, '25).
The cells and nuclei show the same arrangement and distribution as described for the carbol-fuchsin preparations.

Dorso-medially the layer is interrupted rostro-caudally by a vessel lying in the floor of the longitudinal sulcus between the colliculi. Laterally it is limited by the optic tract and the lateral geniculate body rostrally, and further caudally by the optic tract, the medial geniculate body, and the inferior brachium respectively.

Layer 2:

It is also a relatively clear zone and is a little broader/

broader than the previous layer. Besides the scattered cells and nuclei this layer consists chiefly of radial fibres along with some irregularly disposed transverse and oblique fibres.

The radial fibres are continuous centrally with similar fibres of the deeper layers; peripherally they enter layer 1. The arrangement of the fibres of this layer resembles the previous layer except that medially and rostrally the layer is continuous with its fellow of the opposite side.

Layer 3:

This layer is not very well defined from the subjacent layers and consists of both radial and transverse fibres arranged into a dense network.

The transverse bundles of fibres are very prominent rostro-laterally and are continuous further laterally with fibres of the optic tract and similarly disposed fibres of the lateral geniculate body and the medial geniculate body; further caudally it is continuous with the outer part of the medial geniculate body and the inferior brachium; still further caudally the colliculo-collicular fibres from the inferior colliculus enter this layer.

Medially the layer converges and is partly interrupted/

rupted by the blood vessel in the floor of the longitudinal sulcus and partly its fibres cross to the opposite side along with the decussating fibres of layer 4.

The radial fibres, on the other hand, are continuous centrally with those of the deeper layers and peripherally with layers 1 and 2.

Layer 4:

It consists of a plexiform network of fibres which are disposed in all directions - transverse, oblique, and radial. This layer, in fact, except in the most rostral part of the superior colliculus, cannot be easily differentiated from the previous layer. The oblique fibres are arranged in small bundles, cut into short lengths.

Rostrally these bundles are in line with well marked fibres of the medial geniculate body laterally and with similarly disposed fibres of the tegmentum ventrally. Further caudally they are in line with fibres of the tegmentum on the medial aspect of the medial geniculate body, and of the inferior brachium. At the most caudal limit of the superior colliculus the colliculo-collicular fibres from the inferior colliculus enter this layer from its lateral aspect.

Medially/

Medially this layer becomes slightly narrower and is continuous with its fellow of the opposite side, the fibres decussating in the median plane.

The radial fibres, as usual, run both centrally and peripherally.

Layer 5:

Like the previous layer this layer, too, consists of radial, oblique and transverse fibres forming a plexiform network. The fibres are arranged in small bundles, cut into short lengths. These bundles are mostly vertical dorso-medially, but oblique ventro-laterally becoming transverse rostrally.

Rostrally the transverse bundles can be followed ventrally into the tegmentum where some of them sweep round the medial side of the medial geniculate body as far as its ventral border entering the latter on the way, while others enter the substantia nigra; a little caudally some of the oblique bundles are in line with the fibres of the medial lemniscus. At the caudal part of the superior colliculus the colliculo-collicular fibres enter this layer laterally.

Medially the layer becomes a little narrower rostrally and is limited by a blood vessel, as stated already, in/

in the floor of the median longitudinal sulcus; more caudally the layer is continuous with its fellow of the opposite side on the dorsal aspect of the posterior commissure, the dorsal fibres of which spread evenly into this layer on each side; still further caudally the layer merges with its fellow of the opposite side in the median plane between the decussating fibres of layer 4 and the tectal commissure of the superior colliculus. Few scattered transverse fibres can be seen to cross the middle line in this layer. Most caudally, however, this layer is greatly narrowed both medially and laterally and is connected by fibres with the inferior colliculus.

The radial fibres, as in the previous layers, are continuous centrally with the deeper and peripherally with the superficial layers.

Layers 6 and 7:

These two layers have been considered together since the transverse fibres, which characterise layer 7, have invaded layer 6 and spread throughout its width. In addition to the transverse fibres there are numerous radial fibres, as well. The fibres of these layers are thicker than those of the other layers. These layers together appear to be a single layer which narrows dorso-medially/

medially but widens out ventro-laterally.

The transverse fibres are arranged in small bundles.

Medially and rostrally the fibres decussate in the posterior commissure; further caudally they do so in the tectal commissure (commissura tecti) of the superior colliculus. At the caudal level of the superior colliculus the fibres decussating in the tectal commissure spread out laterally into the inferior colliculus as colliculo-collicular fibres.

Ventrally the fibres spread out into layer 5 and then enter the tegmentum as tecto-tegmental, tecto-bulbar, and tecto-spinal tracts. The more medial fibres rostrally entering the tegmentum bend medially and decussate in the median plane in the dorsal tegmental decussation. Some of these fibres enter the oculomotor nucleus and the medial longitudinal bundle. The intermediate fibres bending medially come into relation with the different neurons of the tegmentum including the red nucleus. These fibres, too, decussate to the opposite side in the dorsal tegmental decussation. The more lateral fibres, on the other hand, curve medially on the medial aspect of the /

the medial geniculate body and inferior brachium to reach the more ventral part of the tegmentum where they come into relation with the neurons of the substantia nigra. More caudally the lateral fibres decussate in the median plane in the ventral tegmental decussation.

Through these dorsal and ventral tegmental decussations the tectum of one side probably comes into relation with the different tegmental neurons of the opposite side.

The radial fibres permeating throughout these layers are continuous peripherally with the superficial layers and centrally with layer 8.

Layer 8:

This is a fairly broad zone consisting of a dense plexiform network of fibres. The fibres are mostly fine in character being intermingled with some coarser fibres.

Dorsally the network is continuous with its fellow of the opposite side in the roof of the aqueduct. Ventrally it does so with the similar network of the periventricular gray of the tegmentum where it is directly continuous with the network of the oculomotor nucleus.

At all levels peripherally the network is continuous with the radial fibres of the more superficial layers.

Rostrally, however, this layer presents mostly vertical/

vertical bundles of fibres, cut into short lengths, particularly in its dorsal part.

Layer 9:

It appears to be a very narrow relatively clear zone encircling the ependymal layer of the aqueduct.

At all levels it consists of a very fine network of fibres being continuous peripherally with the superficial layers. Dorsally it is continuous with its fellow of the opposite side, while ventrally it is continued into the tegmentum crossing to the opposite side in the floor of the aqueduct.

Layer 10:

This layer consists of one to three rows of oval nuclei, their long axes being parallel to the surface of the aqueduct. The layer is devoid of any fibres.

B. INFERIOR COLLICULUS.

The inferior colliculus, on the other hand, does not present the marked stratification of cells and fibres shown by the superior colliculus.

The deeper layers of the superior colliculus i.e. layers 7, 8, 9, and 10 are still represented in the inferior/

inferior colliculus; but the more superficial layers i.e. layers 2, 3, 4, 5, and 6 are replaced at this level by an oval mass of diffusely scattered cells and nuclei with its long axis vertical in transverse section. This oval mass constitutes the most important part of the inferior colliculus and is termed its nucleus. The stratum zonale of the superior colliculus is also represented in the inferior colliculus.

Thus though the main nuclear mass of the inferior colliculus, unlike the superior, is completely devoid of stratification of cells and fibres, yet considered as a whole from the surface to the ependyma of the aqueduct, it can be differentiated into the following six layers:

1. Stratum zonale.
2. Nucleus of the inferior colliculus.
3. Stratum album centrale.
4. Stratum griseum periventriculare.
5. Stratum fibrosum periventriculare.
6. Stratum ependymale.

Carbol-fuchsin preparations (Figs. 45, 46).

Layer 1:

It is a narrow relatively clear peripheral zone and corresponds/

corresponds with that of the superior colliculus in the character and distribution of the cells and nuclei.

Dorsally it is continuous with its fellow of the opposite side and ventrally with the tegmentum.

Layer 2 (Nucleus of the inferior colliculus).

This constitutes the chief and the most characteristic zone of the inferior colliculus. In transverse section it presents an oval outline with its long axis vertical (as already stated). The cells and nuclei without apparent cytoplasm replace layers 2 to 6 of the superior colliculus and are arranged very diffusely with distinct intercellular spaces between them. The cells are mostly of the small stellate type containing a few Nissl granules. A large number of large stellate cells containing multiple Nissl granules are also scattered throughout the mass. They are more numerous in the rostral than in the caudal part of the inferior colliculus. The nuclei without apparent cytoplasm are small, round, and oval in shape containing single or multiple distinct particles. Some of these nuclei are a little larger than the rest.

Caudally the nuclear mass is continuous with its fellow of the opposite side in the roof of the aqueduct, but rostrally it is connected by a zone of more diffusely scattered/

scattered cells and nuclei which are arranged in horizontal rows.

Rostrally and ventro-laterally it merges with a group of neurons of the tegmentum lying just deep to the surface. These latter neurons probably form part of the nucleus of the lateral lemniscus within which they lie. Ventro-medially, however, it is separated from the reticular formation of the tegmentum by a fibre zone, which, in these preparations, consists of more diffusely scattered cells and nuclei.

Rostrally and medially the nuclear mass is separated from the stratum griseum periventriculare by the stratum album centrale, but more caudally it seems to be in continuity with the stratum griseum periventriculare.

Layer 3:

This layer is homologous with layer 7 of the superior colliculus both in character and in disposition of its contained cells and nuclei. It is narrower dorsally but broader ventrally. It appears to be a relatively clear zone because of the more diffuse character of cells and nuclei.

Layer 4:

This layer corresponds with layer 8 of the superior colliculus/

colliculus in all respects except that it is a little narrower, particularly dorsally. Ventrally in the tegmental continuation of this layer lie the large stellate cells of the trochlear nucleus.

As in the superior colliculus the large rounded and piriform cells of the mesencephalic nucleus of the trigeminal nerve lie scattered in the peripheral zone of this layer. They are distributed mostly in the tegmental continuation of this layer except rostrally where a few cells can be found to be present in the tectal region. The cells can be traced as far back as the caudal region of the inferior colliculus.

Layers 5 and 6:

These layers respectively are in agreement with layers 9 and 10 of the superior colliculus in all respects.

Iron-haematoxylin preparations.

Layer 1:

Rostrally it consists of small bundles of oblique fibres, cut into short lengths, and directed upward and outward; but caudally the fibres are transversely disposed. Ventrally the fibres are more or less vertical and merge with those of the lateral lemniscus. Dorsally this/

this layer merges with its fellow of the opposite side, the fibres decussating in the tectal decussation of the inferior colliculus. Fibres from layer 2 also enter this layer freely.

From their continuity with the lateral lemniscus these fibres appear chiefly to be lemniscal in nature on their way to the medial geniculate body through the inferior brachium, some fibres from layer 2 also accompanying them.

Layer 2:

This layer consists of a dense plexiform network of fine fibres, the density of which is greatest in the ventral half of the nuclear mass where the fibres of the lateral lemniscus enter it. The network shows some distinct transverse and radial fibres as well.

The transverse fibres appear in small bundles and traverse throughout its entire extent. Dorsally and medially they decussate in the median plane in the tectal decussation of the inferior colliculus. It is through these fibres, probably intercollicular in nature, that this nuclear mass establishes communication with its fellow of the opposite side. Laterally, however, they bend downward and outward and are in a line with the fibres/

fibres of the lateral lemniscus, which probably also decussate to the opposite side. Rostrally it is connected with the superior colliculus by colliculo-collicular fibres.

The radial fibres, on the other hand, are innumerable, usually appear singly, and are continuous centrally with similar fibres of the deeper zones.

Layer 3:

This layer is narrower dorsally but broader ventrally. It consists of both transverse and radial fibres, the former forming the most characteristic feature. It gradually narrows down caudally.

Dorsally the transverse fibres decussate to the opposite side in the tectal decussation of the inferior colliculus, but further caudally this decussation stops short. Ventrally they enter the tegmentum where they are placed on the medial side of the lateral lemniscus. Ultimately they bend medially passing dorsal to the cortico-spinal fibres and decussate in the median plane in the ventral tegmental decussation.

The radial fibres are numerous and at all levels enter superficially the nuclear mass and centrally are continuous /

continuous with the periventricular network of fibres. Caudally, however, they sweep outward along the ventral aspect of the nuclear mass.

Layer 4:

This is homologous with layer 8 of the superior colliculus and corresponds to that layer in all respects except that in the tegmental continuation of the layer ventrally it is directly continuous with the network of the trochlear nucleus. As in the superior colliculus the network is continuous peripherally with the radial fibres, described already.

Rostrally the deeper part of this zone presents small bundles of transverse and oblique fibres. At all levels the fibres of the deeper zone are continuous with the superficial plexiform network.

The transverse fibres of the trochlear nerve, cut into short lengths, are seen to traverse the peripheral zone of this layer superficial as well as deep to the mesencephalic roots of the trigeminal nerve, which appear as small areas of transversely cut fibres.

Layers 5 and 6:

These layers are homologous with layers 9 and 10 of the superior colliculus in all respects.

Silver preparations./

Silver preparations.

Layer 1:

The fibre bundles constituting this layer are small and cut into very short lengths. Dorsally and rostrally the bundles are oblique with obliquity directed upward and outward, but further caudally they are more or less transverse. Ventrally, however, the bundles are vertical rostrally, but oblique caudally.

Dorsally the layer merges with its fellow of the opposite side, the fibres decussating in the median plane. Ventrally the general drift of the fibres is in a line with the fibres of the lateral lemniscus. Medially the fibres merge with those of layer 2 (the nuclear mass).

Layer 2:

It consists of a dense network of fibres which are distributed in all directions, transverse, radial, oblique and vertical. The transverse fibres, however, constitute the most characteristic feature of this nuclear mass. They traverse the nuclear zone crosswise and decussate dorso-medially in the tectal decussation of the inferior colliculus. On the peripheral part of the nuclear mass some of these fibres bend ventralward and are in a line with fibres of the lateral lemniscus, which probably also decussate/

decussate in this way to the opposite side.

At all levels the radial fibres freely enter the nuclear mass from the deeper zones.

The fibres of the lateral lemniscus enter this zone ventrally.

Layer 3:

This layer is narrower dorsally but broader ventrally. It consists of both transverse and radial fibres, the former constituting the most prominent feature. Caudally this layer thins out gradually in the dorso-ventral direction.

The transverse fibres decussate dorsally in the tectal decussation of the inferior colliculus. Ventrally they enter the tegmentum on the medial side of the lateral lemniscus to come into relation with the different tegmental neurons.

The radial fibres are continuous centrally with the plexiform network of layer 4 and peripherally enter layer 2, the nuclear mass of the inferior colliculus. Caudally, however, they sweep peripherally along the ventral border of the nuclear mass.

Layer 4:

This /

This layer, being homologous with layer 8 of the superior colliculus, corresponds with the latter in all respects except that it is a little narrower and its network of fibres is continuous ventrally with the tegmentum where it joins the network of the trochlear nucleus.

The mesencephalic roots of the trigeminal nerve appear as little segments of fibres being scattered into small areas of different dimensions at the peripheral parts of this layer. The transverse fibres of the trochlear nerve, cut into short lengths, are placed on each side of the mesencephalic roots of the trigeminal nerve on their way dorsalward.

Layers 5 and 6:

These layers correspond respectively in all respects with layers 9 and 10 of the superior colliculus.

REVIEW OF THE OBSERVATIONS.

1. The tectum is that part of the mid brain which lies dorsal to the transverse plane passing through the sulcus limitans of the aqueduct. It consists of a pair of superior colliculi and a pair of inferior colliculi/

colliculi, symmetrically developed, and separated by a cruciate sulcus. The sulcus round the superior colliculus is homologous with the sulcus limitans optici of the submammals.

2. The size of the colliculi is very small in comparison to the cerebrum and the cerebellum, which almost completely overlap them except the dorsal parts of the inferior colliculi, which can still be seen from the surface.

3. The tectum does not contain any cavity or ventricle.

4. Superior colliculus

A. Lamination.

Ten layers have been described from the surface to the ependyma of the aqueduct. ~~This has particularly been made~~ These have been determined from the iron-haematoxylin preparations as in the carbol-fuchsin and the silver preparations the lamination is very indefinite.

B. Cyto-architecture.

(a) The cells are mostly multipolar in nature belonging to the small stellate type; a large number of large stellate cells is also present here and there particularly in layers 5, 6, and 7

(b) /

(b) Layers 2 to 6 merge caudally with layer 2 (the nuclear mass) of the inferior colliculus.

(c) The cells of layer 7 are widely separated by well spaced intervals.

(d) The mesencephalic nuclei of the trigeminal nerve appear as large rounded and piriform cells scattered singly in the peripheral part of layer 8 mostly in its tegmental continuation, but a few are also found in the tectal area in the caudal part of the superior colliculus.

(e) Proliferation of the ependymal cells at the level of the posterior commissure forms the sub-commissural organ.

C. Fibro-architecture /

C. Fibro-architecture.

(a) Layers 1 and 2 do not contain any myelinated fibres stainable with iron haematoxylin, but consist of fine unmyelinated fibres, or fibres too thinly myelinated to stain with iron haematoxylin.

(b) The myelinated fibres of the stratum opticum are represented in layer 3. They are more deeply placed in this form than in the submammals.

(c) The fibres of layers 4 and 5 decussate freely in the tectum and the posterior commissure.

(d) The fibres of layer 7 form the respective tecto-bulbar and tecto-tegmental tracts, which not only establish communication with the different tegmental neurons of the same side, but also decussate in the dorsal and ventral tegmental decussations thereby coming into relationship with the tegmental neurons of the opposite side as well.

The /

The fibres of this layer decussate further in the tectal as well as in the posterior commissure. By these tectal and tegmental decussations a widespread bilateral correlation has been established between the two colliculi.

The fibres of the dorsal tecto-bulbar tract come into direct relationship with the medial longitudinal bundle and the oculomotor nucleus; but no direct connection can be traced to the trochlear nucleus. Probably both the oculomotor and the trochlear nuclei receive connexions from the superior colliculus through the medial longitudinal bundle.

(e) The radial fibres are distributed through the different layers of the superior colliculus. Centrally they communicate with the periventricular network and peripherally extend up to layer 1 as shown in the /

the silver preparations.

(h) Caudally the superior colliculus is connected with the corresponding inferior colliculus by the colliculo-collicular fibres.

5. Inferior Colliculus.

A. Lamination.

The inferior colliculus does not show so well marked lamination as the superior colliculus; but still the layers 1, 7, 8, 9, and 10 of the superior colliculus are well represented in the inferior colliculus. Layers 2 to 6 of the superior colliculus, however, are replaced here by a homogeneous oval mass of diffusely scattered cells and nuclei which constitute the nuclear mass of the inferior colliculus. Thus from the surface to the ependyma of the aqueduct the inferior colliculus shows only six layers.

B. Cyto-architecture.

(a) The cellular architecture of layers 1, 3, 4, 5, and 6 corresponds in all respects to the layers 1, 7, 8, 9, and 10 of the superior colliculus./

culus.

(b) The nuclear mass (layer 2) consists chiefly of small stellate cells; but a great number of large stellate cells are also present scattered throughout the mass, more in the rostral than in the caudal part of the inferior colliculus. The cells are arranged in a diffuse manner with distinct intercellular spaces between them.

(c) The cells of the mesencephalic nucleus of the trigeminal nerve can be traced as far back as the caudal limit of the inferior colliculus. They are present singly in the peripheral zone of layer 4 mostly in its tegmental continuation, but rostrally a few cells can be found in the tectal region as well.

C. Fibro-architecture /

C. Fibro-architecture.

(a) The myelinated fibres of layer 1 belong partly to the lateral lemnisuc and partly to the fibres of the nuclear mass (layer 2).
The fibres of this layer decussate to the opposite side in the wall of the tectum.

(b) The plexiform network of the myelinated fibres of the nuclear mass is denser in its ventral half. Dorsally the network is connected with its fellow of the opposite side by inter-collicular fibres, ventrally with fibres of the corresponding lateral lemniscus, and centrally with the deeper layers by the radial fibres.

(c) The fibres of layer 3 are also myelinated. They decussate dorsally in the tectal commissure of the inferior colliculus and ventrally enter the tegmentum to come into relation with its different neurons.

(d) Layers 4, 5 and 6 correspond in all respects with layers 8, 9, and 10 of the superior colliculus except that the plexiform network of layer 4 is connected in its tegmental continuation with similar network of the trochlear nucleus.

(e) /

(e) The nuclear mass of the inferior colliculus is thus encircled on all sides by a zone of myelinated fibres which appear to form a surrounding capsule for it.

DISCUSSION AND CONCLUSION

DISCUSSION AND CONCLUSION

From the description of the representative brains of the vertebrate series it is evident that the optic lobes (corpora bigemina), which comprise the dorsal part of the mid-brain in the submammals, are very well developed in all the brains examined.

The pia mater covering the superficial surface of the optic lobe in the salmon, frog, and lizard is pigmented, but in the domestic fowl and the white rat it is non-pigmented in character.

In the submammals each optic lobe is encircled by a circular sulcus, the sulcus limitans optici. This sulcus demarcates the optic lobe from the surrounding parts and is more marked ventrally. In the white rat, however, it is represented by the sulcus round the superior colliculus, part of which helps to form the cruciate sulcus separating the corpora quadrigemina in the mammals.

In the salmon, frog, and lizard the optic lobes are placed one on each side of the median plane being partially fused with each other dorsally, a median longitudinal sulcus intervening between them on the surface. In the domestic fowl the lobes have deviated away from the middle line being situated one on each side of the brain stem. In the white rat, on the other hand, the superior and the inferior colliculi are again fused with one another in the

median plane constituting the tectum and forming the roof of the aqueduct.

Fig.47 presents outline drawings from the photographs showing the lateral surfaces of the representative brains of the vertebrate series - pisces (salmon parr), amphibia (frog), reptilia (green lizard), aves (domestic fowl) and mammal (white rat). The lengths of the brains have been kept the same in all cases either by reduction or by magnification of their sizes to give an approximate idea of the relative size of three fundamental parts of the brain - cerebrum, optic lobe and cerebellum, as seen from the surface. It is evident from the figure that in the pisces (salmon parr) the optic lobe appears to dominate the entire brain, forming the largest of these parts. Both the cerebrum and the cerebellum are relatively much smaller in size, the former particularly being very poorly developed and forming the smallest part. The optic lobe lies in contact with the cerebrum and the cerebellum, but is not overlapped by them. In the amphibia (frog) the cerebrum shows more growth, and presents a smooth surface. The optic lobe, though well formed, is relatively to the cerebrum, smaller than in the fish. It is separated from the cerebrum by the diencephalon which is visible from the dorsal aspect. The cerebellum is very poorly developed and appears as a thin flattened structure lying in contact with the optic lobe caudally.

In the reptilia (green lizard), as in the frog, the cerebrum still presents a smooth surface, and the size of the optic lobe, relative to that of the cerebrum, is again smaller. But the diencephalon in this form, unlike that of the frog, cannot be seen on the surface between the optic lobe and the cerebrum. The optic lobe is partially overlapped rostrally by the cerebrum and caudally by the cerebellum, which is still very poorly developed appearing as a thin, smooth, and flattened structure forming the smallest part of the brain. In the aves (domestic fowl) the cerebrum shows marked accentuation of growth although it still presents a smooth surface. The size of the optic lobe, relative to that of the cerebrum, is still smaller; it is even smaller than that of the cerebellum, which shows more growth in this form and presents fissures. The optic lobe, unlike that of the lizard, is markedly overlapped by the cerebrum and the cerebellum. In the mammal (white rat) the cerebrum shows enormous growth, its surface being still smooth in the rat, and forms the largest and the most dominant part of the brain. The tectum is markedly reduced in size and constitutes the smallest of the three parts of the [illegible] brain, being almost completely overlapped by the cerebrum and the cerebellum except the dorsal parts of its inferior colliculi, which are visible from the surface. Richard Owen ('68), who made the same observation, stated

that the 'bigeminal' bodies are more or less exposed on the surface between the cerebral hemispheres and the cerebellum in all marsupials, in many rodents, in all insectivores, and in bats. The sizes of the superior and the inferior colliculi very in different mammals (R. Owen, '68; St.George Mivart, '81; Kappers, Huber and Crosby, '36). In the white rat, however, the author has noted that the inferior colliculi present more marked dorsal prominences than the superior, being smaller antero-posteriorly but larger vertically than the latter.

Comparing in this way the optic lobes in the different representative brains of the vertebrate kingdom there is evidence from the above that the size of the lobes, as observed from the surface and relative to the size of the cerebrum, is largest in the fish; as evolution proceeds to the higher orders, it undergoes a process of regression in size, relative to that of the cerebrum. This has reached its maximum in the mammals, where the equivalent of the sub-mammalian optic lobes, the tectum, has been reduced to the minimum size. This is particularly true of the superior colliculi, which are homologous with the optic tectal parts of the optic lobes of the submammals. This gradual reduction in size of the optic lobes in phylogeny is also evident in the ontogeny of the bird's brain, where the size of the optic lobe, relative to that of the cerebrum, diminishes

as age advances. Comparing the brains of a one day old chick and an adult fowl (2 yrs. +), it is quite clear that the growth of the cerebral hemisphere is much greater than that of the optic lobe (Figs.24, 26). This has also been stated by E. Sutler ('43) in his observations on the bird's brain as follows, "the corpora bigemina and the cerebral hemisphere increase markedly in size in the first third or in the first half of the embryonic period - the growth of the corpora bigemina is considerably smaller in the later embryonic and the whole post embryonic period than that of the hemispheres and the cerebellum". Thus it appears that when the brains of the vertebrate series are brought to the same length, the size of the optic tectum, relative to that of the cerebrum, as indicated by the extent of their free surfaces, diminishes as the vertebrate series is ascended. Quantitative estimations of the volume of the optic tectum, either absolute or relative to that of the whole of the brain, have not, however, been made.

Each optic lobe in the submammals contains a cavity, the optic ventricle, which not only communicates with its fellow of the opposite side forming a common ventricular cavity but also communicates with the aqueduct of the mid-brain. The optic ventricle thus appears to be an extension of the aqueduct as noted by de Lange ('10) in his description

of the brains of the selachians, teleosts, and ganoids. The author agrees with C.J. Herrick ('17), however, that the lateral recess of the ventricle does not represent the sulcus limitans. This sulcus lies in the lateral wall of the aqueduct ventral to the torus semicircularis and is specially marked in the frog, less so in the lizard, and is very indefinite in the fish and the bird. In the mammals its position in the lateral wall of the aqueduct, ventral to the inferior colliculus, is quite in agreement with its position in the submammals, where it lies ventral to the torus semicircularis, a structure homologous with the inferior colliculus of the mammals.

The optic ventricle is very well developed and widely dilated in the fish, frog, and lizard. This has also been described by C.J. Herrick ('17) in Necturus. It is slit-like in the birds, and the author has noted in agreement with Kappers, Huber and Crosby ('36), that this slit-like form might be interpreted as a distortion of the ventricle associated with the ventro-lateral shifting of the optic lobes. Finally, it is to be remarked that the tectum in the mammals, as represented by the white rat, contains no ventricle.

The optic ventricle divides each optic lobe in the submammals into a roof, the optic tectum, and a floor, the torus semicircularis, which merges with the tegmentum of the mid-brain. In the lower vertebrates the optic tectum

receives for the most part optic fibres. This is particularly true in the teleost brain, as Belloncí ('88) and Ariens Kappers ('29) have already pointed out. For this reason the author considers that the optic tectum in the submammals should not be called merely "the tectum", as suggested by some workers, since the tectum in the mammals includes both the superior and the inferior colliculi. The torus semicircularis of fish, amphibians and reptiles has been so called because it forms a semicircular elevation in the floor of the optic ventricle. It has, however, been named differently by different observers - e.g. "colliculi" by Rabl Rückhard and C.L. Herrick as stated by Kappers ('06), "inferior collicular eminence" by Kappers ('20, '21, '29) and Shanklin ('30), "colliculi posteriores" by A.Frederikse ('31), and "corpus posterius" by Huber and Crosby ('36). In the bird its homologue, though described as having the same position and connections, has been called the ganglion laterale by Wallenberg ('98) and nucleus mesencephalicus lateralis pars dorsalis by Ariens Kappers ('21).

In the teleost the optic ventricle is very well developed and extends to the caudal limit of the optic lobe. The torus semicircularis lies in the floor of the optic ventricle throughout its rostro-caudal extent and is under cover of the optic tectum. Unlike that of the frog and the lizard, it does not approach the median plane to undergo fusion with its fellow of the opposite side. It is further

demarcated into a medial and a lateral eminence by a ventricular groove - this division, however, is not found in the other submammals. It is very probable that the medial approach of the torus semicircularis in this form has been prevented by the valvula of the cerebellum, a structure conspicuous in the teleost and described by Ariens Kappers ('29) as the rostral extension of the basi-auricular part of the cerebellum into the optic ventricle. The fusion of the valvula of the cerebellum with the medial eminence of the torus semicircularis divides the aqueduct from the common ventricular cavity.

The torus longitudinalis is another structure conspicuous in the teleost fish and is absent in the other representative vertebrate brains. It appears as a median outgrowth from the roof of the optic ventricle. According to Ariens Kappers ('29) it arises from the deeper granular layer of the optic tectum. The author, however, does not agree with this view; from the point of view of gross anatomy and histology the torus longitudinalis, in his opinion, is formed by the fusion in the median plane of two separate processes protruding into the ventricle from the dorso-medial part of the optic tectum, all the layers of which are represented in its formation. This is partially in agreement with Kappers, Huber and Crosby ('36). The author is, however, of the same opinion as Kappers ('29) that it

is larger rostrally gradually diminishing in size caudally where the two halves remain separate. The torus longitudinalis is absent in the selachiens (Kappers, '06).

In the frog, as in the fish, the tori semicirculares lie under cover of the optic tectum throughout their rostro-caudal extent. The wide and well formed optic ventricle, unlike that of the fish, does not extend to the caudal limit of the optic lobe but stops short a little behind the level of fusion of the tori semicirculares, which, bulging into the optic ventricle, fuse in the median plane at the rostral level of the trochlear nucleus separating thereby the optic ventricle from the aqueduct. The fused tori form the roof of the aqueduct as do the inferior colliculi in the mammals.

In the lizard, too, as in the frog, the optic ventricle is wide, and does not extend to the caudal limit of the optic lobe; unlike the frog it stops short farther rostral:ward just at the site of fusion of the tori semicirculares, which meet and fuse with each other in the median plane at the caudal level of the oculomotor nucleus forming the roof of the aqueduct. Unlike the frog, however, they are not covered by the optic tectum throughout their rostro-caudal extent, their most caudal parts being exposed to the surface behind the optic tectum lying under cover of the cerebellum - a condition very like that of the inferior colliculi of the mammals. This is also in agreement with A. Frederikse ('31) and Huber and Crosby ('33).

In the bird the optic ventricle is slit-like as though stretched in association with the divergence of the optic lobes. As in the frog and in the lizard, it does not extend to the caudal limit of the optic lobe. The nucleus mesencephalicus lateralis pars dorsalis, homologous with the torus semicircularis, lies completely under cover of the optic tectum as in the fish and the frog; but unlike the frog and the lizard, it does not approach the middle line to fuse with its fellow of the opposite side. This also might be associated with the ventro-lateral shifting of the optic lobes in the bird.

In the white rat the tectum is comprised of a pair of superior and a pair of inferior colliculi, which form the roof of the aqueduct, and, unlike the optic lobes of the submammals, does not contain a ventricle. The colliculi are fused without overlapping, a cruciate sulcus demarcating them on the surface.

Comparing now the optic tectum, the torus semicircularis and the optic ventricle in the representative brains of the vertebrate series it is evident from the above that the optic tectum in the fish and the frog submerges the torus semicircularis completely (Fig.48). It has begun to regress in the lizard, in which the most caudal part of the torus semicircularis, being released from the covering of the optic tectum, appears on the surface behind the latter as

the forerunner of the inferior colliculus of the mammals. This process of regression has reached its climax in the mammals where the superior colliculus (homologous with the optic tectum of the submammals) lies entirely rostral to the inferior colliculus, which is thus completely released of its covering. The corpora bigemina of the submammals are thus replaced by the corpora quadrigemina of the mammals.

In the bird, however, none of these structures, the optic tectum, the torus semicircularis, and the optic ventricle, can be placed as a stage intermediate between that of the reptiles on the one hand and that of the mammals on the other. It can also be said that in the structure of its mid-brain a lizard is more akin to a mammal than to a bird.

It is further evident from the above that the optic tectum and the torus semicircularis of the submammals appear to be homologous respectively with the mammalian superior and inferior colliculus. This view of the homologies of the submammalian torus semicircularis with the avian nucleus mesencephalicus lateralis pars dorsalis and the mammalian inferior colliculus, though supported by Kappers ('21) and Huber and Crosby ('33), has, however, been questioned on embryological grounds by Palmgren ('21) in the development of the bird.

Thus, in general agreement with de Lange ('10), it can

be concluded from the foregoing discussion that the evolution of the mammalian tectum may have been characterised by the following changes:

(a) The submammalian optic tectum became the superior colliculus of the mammals.

(b) The torus semicircularis of the submammals, on the other hand became the inferior colliculus of the mammals.

The histological studies of the representative brains of the vertebrate series show that the optic tectum in all cases presents lamination of the contained cells and fibres. All previous workers agreed on this point, but classified the layers differently. According to the Spanish School (P. Ramon, '90, '96, '98 and '99; Ramon y Cajal, '91, '99 and '09 - '11), the different layers have been named numerically from within outwards in all the representative brains except in the bird, where this has been done in the reverse order, i.e. from without inwards, but no reasons for the difference in the order have been given. The author, like most of the recent workers has numbered the layers from without inwards. Further the layers have been correlated with the six fundamental strata of the reptilian tectum as described by Huber and Crosby ('33), namely: (i) stratum opticum, (ii) stratum fibrosum et griseum superficiale, (iii) stratum griseum centrale, (iv) stratum album centrale, (v) stratum griseum periventriculare, and

Table 9. Table showing the different layers of the optic tectum in the representative brains of the vertebrate series and their homologies

Name of the animal	Total number of layers	Stratum zonale	Stratum opticum	Stratum fibrosum et griseum superficiale
Fish (Salmon parr)	10	Layer 1	Layer 2	Layers 3 - 6 (= 4 layers)
Frog	15	Layer 1	Layer 2	Layers 3 - 6 (= 4 layers)
Lizard	16	Layer 1	Layer 2	Layers 3 - 7 (= 5 layers)
Bird (Domestic fowl)	16	-	Layer 1	Layers 2 - 10 (= 9 layers)
White	10	Layer 1	Layer 3	Layers 2, 4 & 5

(cont'd.) /

Table 9. (Cont'd.)

Stratum griseum centrale	Stratum album centrale	Stratum griseum periventri: culare	Stratum fibrosum periventri: culare	Stratum ependy: male
Layer 7	Layer 8	Layer 9	-	Layer 10
Layer 7	Layer 8	Layers 9 - 13 (= 5 layers)	Layer 14	Layer 15
Layer 8	Layer 9	Layers 10 - 14 (= 5 layers)	Layer 15	Layer 16
Layer 11	Layers 12 & 13	Layer 14	Layer 15	Layer 16
Layer 6	Layer 7	Layer 8	Layer 9	Layer 10

(vi) stratum fibrosum periventriculare. Huber and Crosby excluded completely the ependymal layer, which has, however, been considered by the author to form the innermost layer of the optic tectum for the following reasons:

(i) The innermost cells of the stratum griseum constitute the ependymal layer in Necturus (Herrick, '17).

(ii) It has been observed by the author that the ependymal cells give off thread like processes, which radiate peripheralward at right angles to the ventricular surface. These processes are clearly evident in the frog and lizard, and have been described by Kappers, Huber and Crosby ('36) as fuzzy processes forming the supporting framework of the optic tectum.

The stratum opticum, in the author's opinion, appears to receive fibres from the marginal optic tract, which reaches the optic tectum ventro-rostrally and gradually spreads in a dorso-caudal direction. This is also in agreement with Huber and Crosby ('33) who further stated that the fibres on their way bend inwards to form synapses with the deeper layers.

The stratum fibrosum et griseum superficiale consists of alternate cell and fibre layers, their number varying in the different representative brains (Table 9). Some of

its transverse fibres seem to belong to the marginal optic tract, while the radial fibres appear to be intrinsic in nature extending between the different layers of the optic tectum. The radial fibres are so conspicuous in the bird that the stratum has been here called "the radial fibre layer" by Cragg, Evans and Hamlyn ('54).

The stratum griseum centrale lies external to the stratum album centrale. The same layer in the bird has been called "the deep plexiform layer" by Cragg, Evans and Hamlyn ('54), but this term, although it is not a misnomer, is confusing since the layer is predominantly composed of cells. This name was given by them probably because the layer is characterised by the presence of a diffuse plexiform network of fibres both in silver and in myelin preparations.

The stratum album centrale lies external to the stratum griseum periventriculare. In all the representative brains it is the most conspicuous of the fibre laters of the optic tectum. Small bundles of transverse and oblique fibres, characterising the layer, decussate dorsally in the posterior commissure and the commisura tecti; ventrally, on the other hand, they decussate in the dorsal and the ventral tegmental decussations.

The stratum griseum periventriculare and stratum fibrosum periventriculare constitute the periventricular components of the optic tectum, the former lying external

to the latter, which lies just outside the ependymal layer lining of the optic ventricle. Both the layers present a plexiform network of fibres. The radial fibres of the layers, particularly of the stratum griseum periventriculare, seem to be continuous with similar fibres of the other layers of the optic tectum.

The stratum ependymale lines the optic ventricle forming the innermost layer of the optic tectum. As already stated it gives off thread-like processes towards the periphery. It further forms the subcommissural organ of Dendy and Nicholls ('10) in all the representative brains of the vertebrate series.

The tectum in urodele amphibia (Necturus), according to C.J. Herrick ('17), presents the most primitive and fundamental histological pattern in phylogeny. According to him the tectum consists of (i) an external fibre layer, the stratum album, and (ii) an internal cell layer, the stratum griseum, the deepest cells of which form the ependymal layer. The most peripheral portion of the stratum album is composed of optic tract fibres, which reach the dorso-medial part of the tectum; the deeper part, on the other hand, which lies just external to the stratum griseum, forms the tractus tecto-peduncularis profundus of Herrick ('17).

With this idea in mind let us consider the optic tectum

of fish (pisces), the lowest class in the vertebrate kingdom. It is evident that in the teleost fish, salmon parr for example, the optic tectum shows more growth and lamination than the urodele, and presents ten layers (Table 10). The stratum zonale (layer 1) forms the most superficial layer and seems to receive fibres from the marginal optic tract ventrally; but according to Kudo ('23a) axons from the torus longitudinalis enter this layer. The author is in agreement with Huber and Crosby ('33, '33a, '34) that the stratum opticum (layer 2) is not demarcated very distinctly from the stratum fibrosum et griseum superficiale (layers 3 to 6). The stratum fibrosum et griseum superficiale consists of four cell and fibre layers. The stratum griseum centrale (layer 7) is very ill-defined. The stratum album centrale (layer 8) is quite distinct, its fibre bundles entering the stratum griseum periventriculare (layer 9) on their way to the tegmentum. The stratum griseum periventriculare is very conspicuous and forms about one-third the total thickness of the optic tectum. It retains still to some extent the primitive character of the urodele optic tectum and consists of closely packed and deeply stained cells, which have not been found arranged in parallel laminae as suggested by Huber and Crosby ('33, '33a, '34). Unlike the frog and lizard, the layer appears single without any lamination. Unlike the other vertebrates, a stratum

fibrosum periventriculare is, however, absent in the salmon parr. This is in agreement with Ramon and Ramon y Cajal ('09 - '11), and Kappers, Huber and Crosby ('36). In disagreement with Kappers, Huber and Crosby ('36) the author finds that the stratum ependymale (layer 10) is very indefinite except in the region of the torus longitudinalis.

Passing now to the frog (amphibia) it is evident that the process of development and growth has advanced to a certain extent. The optic tectum has now fifteen layers (Table 10). This increase in the number of layers, in this form, is due entirely to the lamination of the stratum griseum periventriculare into five alternate cell and fibre layers (layers 9 to 13), which are thus well developed in the frog. The cells of the stratum griseum periventriculare resemble those of the fish. The stratum fibrosum periventriculare (layer 14), which is absent in the fish, is quite distinct in this form. The stratum ependymale (layer 15), unlike that in the fish, is well defined in the frog and its thread-like processes spreading to the periphery are quite evident. The most superficial layers (layers 1 to 8) are homologous with those of the fish, but show the following differences:

(i) The stratum album centrale (layer 6) is more developed containing a greater number of fibres.

Table 10 Table showing the different layers of the optic tectum in the representative brains of the vertebrate series and their homologies.

Name of Animal	Total no. of layers	Stratum zonale	Stratum opticum	Stratum fibrosum et griseum superficiale	Stratum griseum centrale	Stratum album centrale	Stratum griseum periventriculare	Stratum fibrosum periventriculare	Stratum ependymale
Salmon parr	10	layer 1	layer 2	layers 3 - 6 (4 layers)	layer 7	layer 8	layer 9	-	layer 10
Frog	15	layer 1	layer 2	layers 3 - 6 (4 layers)	layer 7	layer 8	layers 9 - 13 (5 layers)	layer 14	layer 15
Green lizard	16	layer 1	layer 2	layers 3 - 7 (5 layers)	layer 8	layer 9	layers 10 - 14 (5 layers)	layer 15	layer 16
Domestic fowl	16	-	layer 1	layers 2 - 10 (9 layers)	layer 11	layers 12 & 13	layer 14	layer 15	layer 16
White rat	10	layer 1	layer 3	layers 2,4,5	layer 6	layer 7	layer 8	layer 9	layer 10

(ii) The stratum griseum centrale (layer 7) presents a broader cellular zone and shows more marked development.

(iii) The cell laminae (layers 3 and 5) of the stratum fibrosum et griseum superficiale are very indefinite consisting of fewer cells scattered very diffusely; the fibre layers (layers 4 and 6), on the contrary, are quite evident and appear to contain a slightly greater number of fibres.

In the lizard (reptilia) the process of growth has advanced still further. The optic tectum now consists of sixteen layers (Table 10). The stratum zonale (layer 1), which, according to the author, forms the most superficial layer, is said to be absent by Huber and Crosby ('33, '33a, '34). The stratum opticum (layer 2) is well developed. The stratum fibrosum et griseum superficiale (layers 3 to 7) consists of five alternate cell and fibre layers instead of four as in the fish or in the frog. Its different layers are not only increased in number but also present more marked growth and definition. The stratum griseum centrale (layer 8) is more developed in this form than in the frog and forms the broadest cellular zone of the optic tectum. The stratum album centrale (layer 9) in like manner shows more growth and definition containing a greater number of fibres. The stratum griseum periventriculare, as in the

frog, consists of five alternate cell and fibre layers (layers 10 to 14), layers 11 and 13 being more developed in this form than in the frog. The stratum fibrosum periventriculare (layer 15) consists of a single layer of plexiform fibres and is more developed in the lizard than in the frog. The periventricular layers are very much better developed in the lizard than in the other representative brains of the vertebrate series. The stratum ependymale (layer 16) does not present, however, any marked change and resembles that of the frog.

In the domestic fowl (aves) the process of development and growth has progressed a further step. The optic tectum has sixteen layers as in the lizard (Table 10); but, unlike the latter, the periventricular cell and fibre layers (layers 14 and 15) are markedly reduced. The stratum fibrosum et griseum superficiale, on the other hand, is most markedly developed presenting the greatest number of laminae found throughout the vertebrate series in this stratum. It presents nine alternate cell and fibre layers (layers 2 to 10) forming about half the thickness of the optic tectum. The stratum opticum (layer 1) has come to the surface in the bird forming the most superficial layer of the optic tectum and is also very well developed. The stratum zonale of still lower forms is either completely absent, or has been replaced entirely by the optic fibres

in the bird. The stratum griseum centrale (layer 11) and the stratum album centrale (layers 12 and 13) are better developed in this form than in the other submammals.

Passing now to the white rat (mammalia), the highest class in the vertebrate phylogeny, it is evident that the lamination of the superior colliculus is reduced once again and there are only ten layers. The fundamental strata of the submammals are still represented in this form, but with certain modifications and their homologies have been shown in Table 10. The stratum ependymale (layer 10) lines the aqueduct forming the innermost layer of the superior colliculus. The stratum fibrosum periventriculare (layer 9) is very poorly developed as in the bird. The cyto-architecture of the other layers is very diffuse making the lamination indefinite and obscure. The stratum griseum (layer 6) and stratum album profundum (layer 7) are homologous with the stratum griseum centrale and stratum album centrale respectively of the submammals, while the stratum griseum superficiale (layer 2), stratum griseum and stratum album mediale (layers 4 and 5) represent the submammalian stratum fibrosum et griseum superficiale and are markedly reduced in this form. The stratum opticum has occupied a deeper position in the white rat and is formed by layer 3 instead of layer 2 as in the fish, frog, and lizard and layer 1 in the bird.

Reviewing the foregoing facts it is clear that the lamination of the optic tectum gradually increases with the progress of evolution in the vertebrate phylogeny attaining its maximum in the reptilia and the aves and undergoing a reduction once again in the mammalia. Thus ten layers in the pisces change to fifteen layers in the frog, sixteen in the lizard and the bird, and ten again in the white rat.

In the fish the torus semicircularis consists of a medial and a lateral eminence. The medial eminence, as stated already, fuses with the valvula of the cerebellum separating thereby the aqueduct from the optic ventricle. The lateral eminence (eminentia lateralis) lies in the periventricular grey in the floor of the optic ventricle and contains an aggregated mass of cells consisting of (i) an incomplete peripheral capsular zone of very closely packed and deeply stained cells, and (ii) a central region where the cells are scattered diffusely. It has been called the nucleus lateralis mesencephali in teleosts (Herrick, '17; Kappers, Huber and Crosby, '36). The cells of the peripheral capsular zone resemble those of the stratum griseum periventriculare of the optic tectum, with which this zone is continuous. The region between this nucleus and the ventricular ependyma, the periventricular layer, is very narrow. The network of fibres of the nuclear mass is connected ventro-laterally with the fasciculus longitudinalis

lateralis (acoustico-lateral lemniscus). This has also been stated by Ariens Kappers ('06, '29), de Lange ('10), C.L.Herrick ('17), and Kappers, Huber and Crosby ('36). The network is further connected with the fibres of the stratum album centrale of the optic tectum, where this lies ventro-lateral to the torus semicircularis.

In the frog, too, the torus semicircularis contains a nuclear mass consisting of (i) an incomplete peripheral capsular zone, and (ii) a deeper central region. The cells of the capsular zone, as in the fish, are closely packed and deeply stained; they resemble those of the stratum griseum periventriculare of the optic tectum, which is, in fact, continuous with the capsular zone. This is in agreement with Kappers, Huber and Crosby ('36). The central region, unlike that of the fish, merges partly with the stratum griseum periventriculare and partly with the stratum griseum et album centrale of the optic tectum. The capsular zone is absent caudal to the site of fusion of the tori semicirculares. The network of fibres of the nuclear mass, more developed than in the fish, is connected ventrally and laterally with the fibres of the lateral lemniscus and tecto-bulbar tract, which, as in the fish, lies on the ventro-lateral aspect of the nuclear mass. The connection of the network with its fellow of the opposite side is more marked in the frog than in the fish; this has been further helped by the fusion of

the respective tori semicirculares. Also the network, unlike that of the fish, is intimately connected with the network of the stratum griseum periventriculare of the optic tectum.

In the lizard the cyto- and fibro-architectures of the torus semicircularis resemble those of the frog in general, but the network of fibres appears to be more distinct than that in the frog. Further the network, unlike that in the frog, is very intimately connected with the similar network of the stratum fibrosum periventriculare of the optic tectum as well as with that of the stratum griseum peri--ventriculare.

In the domestic fowl the nucleus mesencephalicus lateralis pars dorsalis resembles the submammalian torus semicircularis in structure and connections and is homologous with the latter. This is in agreement with Ariens Kappers ('21). As in the other submammals, it consists of (i) a peripheral capsular, and (ii) a deeper central region. The author has observed that the cellular capsular zone of the other submammals is replaced, in this form, by fibres. This is not in agreement with Kappers, Huber and Crosby ('36), who, however, have described a capsular zone consisting of middle-sized cells. The deeper central region is massive being more developed than in the other submammals and as in the latter consists of scattered cells, which resemble those of

the stratum griseum periventriculare of the optic tectum being continuous with the latter. Ventro-laterally the network of fibres of the nucleus mesencephalicus lateralis pars dorsalis is connected with the lateral lemniscus and the tecto-bulbar tract, which, unlike that of the other submammals, courses ventro-medial to it. The author considers that the ventro-medial position of the tecto-bulbar tract in relation to this nucleus in the bird, in contrast to its ventro-lateral position in the other submammals, is probably associated with the ventro-lateral shifting of the optic lobe, already mentioned. The network, unlike that of the frog and the lizard, is connected with its fellow of the opposite side through the posterior commissure as well as through the tectal and the tegmental decussations.

In the white rat the inferior colliculus presents an almost similar histological picture to that of the nucleus mesencephalicus lateralis pars dorsalis of the bird and is comprised of a nuclear mass consisting of (i) a narrow peripheral capsular fibre zone, and (ii) a central region, which, as in the bird, is a massive structure consisting of diffusely scattered cells and nuclei. This region, like that of the frog and the lizard, but unlike that of the bird, is continuous with its fellow of the opposite side along the roof of the aqueduct. It further merges rostrally with

layers 3 to 6 of the superior colliculus. The histological appearances suggest to the author that some fibres of the lateral lemniscus enter the inferior colliculus ventrally, while others enter its superficial capsular zone. The deeper capsular zone, on the other hand, appears to the author to consist of tecto-tegmental fibres. Moreover the inferior colliculi are connected by inter-collicular fibres; these seem to include also a few fibres of the lateral lemniscus reaching thereby the contra-lateral inferior colliculus. Further each inferior colliculus is connected with the homolateral superior colliculus by collicule-collicular fibres.

From the above considerations it is evident that the torus semicircularis of the submammals and the inferior colliculus of the mammals are homologous with each other.

SUMMARY

1. The materials consisted of 20 Salmo salar (salmon parr), 12 Rana temporaria (frog), 12 Lacerta viridis (common green lizard), 45 Gallus domesticus (domestic fowl), and 20 Mus norvegicus albinus (common white rat).

2. The brains, having been fixed by injection with 10% neutral formol-saline, were carefully dissected out. Some measurements and photographs were made, and the specimens were embedded in paraffin cutting down the time of dehydration in the higher grades of alcohol to a minimum and avoiding cedar-wood oil as a clearing agent for reasons which have been given in the text. Three series of serial sections, cut at 15 μ, were prepared from each brain embedded, and were respectively, (a) impregnated with silver by the Bodian method, (b) stained with carbol fuchsin and (c) stained with iron haematoxylin. One hundred and two such series were prepared.

3. The following conclusions were reached:

(a) The size of the optic lobes, as observed from the surface and relative to the size of the cerebrum, was found to diminish as the vertebrate series of brains was ascended. Estimations of the volume of the optic lobes were, however, not made.

(b) It was verified that the superior and the inferior colliculi of the mammals are homologous respectively with the optic tectum and the torus semicircularis composing the submammalian optic lobe. Further, it was found that structurally the optic lobes (including the ventricles) of the pisces, amphibia and reptilia, and the tectum of the mammalia could be arranged in this order as a series. The optic lobes of the aves were, however, divergent, in that they could not be placed in the series as an intermediate stage between the reptilian and mammalian forms.

(c) Throughout the vertebrate series the optic tectum including the superior colliculus of mammals presents a lamination of its constituent cells and fibres. The layers of the representative brains were numbered from without inwards and were compared and correlated with each other using Huber and Crosby's classification of the layers in the reptilian optic tectum as a standard. The lamination of the optic tectum at first increases as the vertebrate series is ascended; it reaches its peak development in the lizard and the bird, and undergoes a reduction again in the mammals.

(d) Homologies in the structure of the torus semicircularis of the lower vertebrates, the nucleus mesencephalicus lateralis pars dorsalis of the aves and the inferior colliculus of the mammalia were noted.

(e) The morphology of the torus longitudinalis, conspicuous in the teleostean fish, was examined. The torus is formed by the fusion in the median plane of two separate processes from the dorso-medial part of the optic tectum, all the layers of which take part in its formation.

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